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Experiments with the Root Excretions of Grasses as a possible means of eliminating *Heterodera schachtii* from infected soil.

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Introduction.

In several previous publications by the present writer reference has been made to the relation between the root excretions of plants and the bionomics of the eelworm *Heterodera schachtii.* Amongst these is a short preliminary note on the significance of the root excretions of certain grasses as a possible means of controlling the nematode. The experiments referred to in this paper having been continued and extended, and the favourable results of the first year's field work having been maintained, a more detailed account of the researches seems to be justified, although the field experiments are still in progress and many aspects of the problem which require laboratory investigation are as yet comparatively untouched. As previously indicated, of the two main lines, chemical and biological, along which investigations must be pursued for a full understanding of the relationship between the reactions of the nematode and the stimulus of the root excretions, the chemical is the more fundamental, and until further work has been carried out from this standpoint much of the biological work is necessarily of an empirical character. It is, however, on purely biological lines that the greatest progress has so far been achieved, and it is with this side of the work solely that the present paper deals.

The phenomenon of specialisation into biological or physiological strains, exhibited by certain nematodes, is particularly marked in the case of *Heterodera schachtii.* Several clearly defined strains which are capable of attacking limited groups of host plants only, and which differ from one another in their physiological responses to various forms of stimulus, exist in Britain. Of these, the widespread potato-strain is at present of the

greatest economic importance, and it is towards the control of this pest that the researches detailed below have been directed. Other strains of the parasite known to exist in Britain show a varying degree of specialisation for peas, hops and mangolds respectively, while sea-marram grass has been found to bear an infection of a *Heterodera* species, most probably *H. schachtii*, on the coast of Devon and near Aberdeen. Studies of the host-ranges of these strains of the nematode have indicated lines of investigation which have led to the experiments with grasses detailed below, but the factors which influence the liberation of the larvae from the cysts remain comparatively obscure for all except the potato-strain, to which alone the use of grass root excretions is applicable as a method of control.

The finding of the apparently indigenous strain of *H. schachtii* parasitic upon sea-marram grass suggested the possibility that this might be the original reservoir of infection to which some at least of the strains of economic importance owed their derivation. Three other findings which seemingly gave support to this view were as follows. Firstly, in the heavily infected field in which the mangold-strain was discovered, among the many species of weeds which were found to be slightly infested were three species of grass. Secondly, pot experiments to discover the range of hosts of economic importance which this strain was capable of attacking, showed that many more larvae were liberated when non-susceptible monocotyledonous plants were grown in infected soil than when non-susceptible dicotyledonous plants were grown. Finally, in a field at Ormskirk infected with the highly specialised potato strain couch grass was found to bear a slight infection of the nematode, although an extensive examination of other weeds failed to reveal any trace of infestation. It was owing to these observations that when experiments on the stimulant properties of potato root excretions with respect to the potato-strain of *H. schachtii* were being carried out, investigations were also begun on the properties of grass root excretions.

Laboratory Experiments.

The general methods adopted in carrying out the laboratory tests were essentially the same as those which have previously been described in connection with the investigations on the properties of potato and mustard

root excretion. The method of obtaining root excretions by growing seedlings in germinating chambers on muslin over distilled water was, however, abandoned early in the work, owing to the poor germination of some species of grass, the seedlings thereafter being grown in pots of soil partially sterilised by steam, the filtered leachings of which contained the root excretions.

Three hundred cysts were used in each experiment as this was considered to be the minimum number from which reliable results could be expected. In this connection an experiment may well be quoted here which was made following a publication by O'Brien and Prentice, in which was quoted the results obtained by a repetition of certain of the present writer's experiments on the effect of mustard root excretion. These repetitions were carried out with fifteen cysts only in each case, although one hundred cysts was the smallest number of cysts used in the original series. In order to test the reliability of results obtained by the use of so low a number as fifteen cysts, a number of fully developed newly formed cysts of approximately equal size ($0{\cdot}6 \times 0{\cdot}5$ mm.) were selected in the autumn from the roots of potato plants grown in infected soil. These were stored through the winter, and in the spring fifteen were placed in each of six petri-dishes to which potato root excretions were added. The petri-dishes were kept in an incubator at 25°C. for three weeks, after which the escaped larvae were counted. The counts obtained were as follows, 285, 975, 226, 130, 147, 352. It was therefore concluded that not less than three hundred cysts should be used for carrying out even roughly quantitative experiments.

The first series of laboratory experiments in which the stimulative effects of grass root excretions were demonstrated was set up with a view to determining whether the potato-strain of *H. schachtii*, like the mangold strain, showed a greater response to non-susceptible monocotyledonous than non-susceptible dicotyledonous plants. Seeds of beet, cabbage, wheat, oats, barley and smooth stalked meadow grass were germinated on muslin stretched over distilled water in petri-dish germinating chambers. When sufficient root development had taken place, five cc. of water was withdrawn from each germinating chamber and placed in a small petri-dish containing 300 cysts, these petri-dishes were then incubated at 25°C. Three hundred cysts in distilled water and in potato root excretions

were similarly treated to serve as controls. At recurrent intervals of seven days counts were made of the escaped larvae and it was found that whereas little hatching took place in response to the wheat, oats, barley, beet and cabbage root excretion, the number of larvae liberated in the meadow grass excretion was just over two-thirds of the number hatched in the potato root excretion. A repetition of this experiment giving a similar result it was decided to test the response of the potato strain of *H. schachtii* to the root excretions of a larger series of grasses.

The grass species selected for trial were those most frequently incorporated in seed mixtures used for short term leys, and were as follows :—*Festuca pratensis*, *F. elatior*, *Dactylis glomerata*, *Anthoxanthum odoratum*, *Poa pratensis*, and *P. trivialis*, *Lolium perennae*, *Avena elatior*, *Phleum pratense* and *Alopecurus pratensis*. Sea-marram grass was also included in some of the earlier tests. The uneven germination of these grasses in the germinating chambers was so great that this method of obtaining root excretions was abandoned and seedlings were grown in pots of soil which had been partially sterilised by steam. The filtered leachings from these pots were thereafter used in all the root excretion tests, for although the amount of root development differed considerably, previous experiments with potato seedlings had shown that only a small trace of root excretion was sufficient to produce the maximum response of the nematodes. Another point which might have led to difficulties in the interpretation of results but for previous experience gained in hatching experiments with potato root excretion was the seasonal fluctuation in the counts. Since all series of experiments were carried out not less than three times and the labour involved in preparation of the experiments and carrying out the actual counts was prolonged, the work extended throughout the spring and summer months of two years. Previous experience in hatching experiments has, however, shown that the maximum rate of hatching is much greater in summer than in the early spring and autumn months, while practically no larvae can be induced to hatch in the winter. Hence each series of experiments had to be considered separately, the only standard of comparison between the series being the proportional number as compared with the controls of potato root excretion and distilled water in each case. Even so, considerable variations were found to occur in the response shown by the nematode to the root excretions of any species of host.

Root excretions of wheat, oats and barley in the leachings of pots of soil proved to have rather more effect in stimulating the nematodes than root excretions obtained from the germinating chambers, but counts of larvae hatched by these cereals were uniformly low as compared with the numbers hatched by certain of the grasses. Consistently high counts of freed larvae were obtained by the use of rough and smooth stalked meadow grass (*Poa trivialis* and *P. pratensis*), the numbers ranging from just under one-third to almost five-sixths of the numbers freed by potato root excretion. Rye grass (*Lolium perennae*) gave the next highest counts, but these in no case exceeded half the number of larvae hatched in the potato root excretion control. Cocksfoot (*Dactylis glomerata*), though markedly less effective than rye grass, shows a slight stimulant action, and on one or two occasions tall fescue (*Festuca elatior*) gave reasonably high counts, but this was not consistent. None of the other grasses which have so far been tried have shown any appreciable stimulant action upon the nematodes except Italian rye grass, which was tested in the later series and proved to be about equal to perennial rye grass in its stimulant effect.

Pot Experiments.

Immediately following the conclusion of the first series of hatching tests, pots of heavily infected soil were sown with each of the grasses used, to determine whether any of them were susceptible to infection. Since the degree of specialisation of the potato-strain is known to vary slightly from district to district duplicate series of pots were sown in soil derived from Yorkshire and South Lincolnshire respectively. Ormskirk soil could not be obtained for this purpose owing to wart disease restrictions. Repeated examinations of the roots of these grasses, which have now been grown for more than three consecutive years in the same soil, have failed to reveal any evidence of cyst formation. Recently, microscopic examinations of stained and cleared roots have been carried out to determine whether any root penetration takes place, for, as Goffart has shown, the larvae of the oat-strain of *H. schachtii* in Schleswig-Holstein penetrate the roots of several weeds belonging to the natural orders Chenopodiaceae and Cruciferae in which they are not able to complete their development. Although other nematodes were found within some of the roots examined no larvae of *H. schachtii* could be found. In order, however, to exclude any

possible errors in diagnosis, pots of partially sterilised soil were very heavily infected with brown cysts isolated from potato roots and were sown with the two species of meadow grass and rye grass. After six months Baermann extractions of the soil showed that numerous larvae had been freed from the cysts, but a particularly intensive search failed to reveal any nematodes within the roots. Grass roots from the field experiments have been similarly examined and have also given negative results. It seems therefore safe to assume that the potato-strain of *H. schachtii*, at least from two districts in England, will not readily attack the grasses mentioned above although the larvae react to the stimulus exerted by the root excretions to the extent of hatching from the cysts.

Before describing experiments dealing with comparisons of the viable contents of cysts before and after soil treatment with grass root excretions some account must be given of the methods used in arriving at the numerical estimations. Detailed counts of the number of unhatched eggs remaining in each cyst were found to be useless as a means of comparison since the original egg content of the cysts varied from less than one hundred to over six hundred, and the empty shells from which the larvae had hatched adhered together in such a way as to make accurate counts impossible to carry out. The following method was therefore adopted and has been used throughout for estimations of cyst contents both in pot experiments and field work. The cysts selected for contents estimation have been as nearly as possible of equal size. Very small cysts and those of oval shape indicating immaturity have been discarded. Each cyst has been dissected in a drop of water under a binocular microscope and has immediately been classified under one of the five headings—full, three-quarters-full, half-full, quarter-full or empty. On the completion of each set of dissections, the percentage of cysts in each category has been worked out and finally a single figure representing the viable contents of the sample as a whole has been determined by expressing the sum of the percentage of quarter-full cysts, twice the percentage of half-full cysts, three times the percentage of three-quarters-full cysts, and four times the percentage of full cysts contained in the sample as a percentage of the figure that would thus have been obtained had all the cysts contained their full complement of unhatched eggs—viz., 400.

A series of pot experiments which demonstrate the reduction in the cyst contents which may be brought about by the use of grass root excretions

under optimal conditions was carried out as follows. Six-inch plant pots of heavily infected soil were sown in January with smooth stalked meadow grass, rough stalked meadow grass, perennial rye grass and sea-marram grass respectively. These were kept in a warm greenhouse for one year and were then turned out, the cysts were recovered from the soil by Morgan's flotation method and their remaining viable contents were estimated and compared with the viable contents of cysts from an untreated sample of the same soil. Of the 500 cysts dissected from the untreated soil which formed the standard of comparison only 33·75% of the eggs were unhatched or viable. Two hundred cysts from each of the pots of soil in which grasses had been grown for a year were dissected and their contents estimated. It was found that in the pot of soil treated with smooth stalked meadow grass 19·37% of the cyst contents remained unhatched, that is, a reduction in the number of unhatched eggs amounting to 42·6% of the number present before the treatment was begun, had been effected in one year. A slightly greater reduction, viz., 43·8% of the original count, had taken place in the soil in which rough-stalked meadow grass had been grown, while the rye grass had reduced the viable cyst contents by 40·4%. Sea-marram grass, which had been selected to serve as a control for this series of experiments, being one of the grasses which had produced no reaction of the larvae in the laboratory tests, was found to have had very little effect on the cyst contents, which in this pot were estimated to be 32·2% viable, a reduction of only 5·5% as compared with the original soil sample. Obviously the rate of emptying of the cysts indicated by these figures was largely the result of the favourable conditions of temperature and moisture prevailing throughout the duration of the experiment, and equally striking results could not be anticipated from a field trial.

Field Experiments.

In January 1931 arrangements were made with a potato grower in South Yorkshire for a full trial of the use of grasses as a method of eelworm elimination to be carried out on a larger scale than could be undertaken at the Institute's Field Station at St. Albans. The two fields selected as most suitable for this purpose were adjacent to one another, both were moderately heavily infected with eelworm, both had been cropped with potatoes in 1930 and showed some evidence of eelworm damage, and would

normally have been under the same four course rotation preparatory to the next potato planting. Winter wheat had been sown as the first rotation crop.

The smaller field of about 16 acres, roughly triangular in shape, was selected for the experiment, and arrangements were made for this to be put down to grass for a period of as many years as was deemed necessary for an adequate trial of the method. The larger field of about 34 acres was to serve as a control, the usual cereal and other crops forming the customary rotation of the district were to be grown.

The first series of soil samples from which the viable contents of the cysts in both fields were to be estimated were taken in January 1931. It was first ascertained that the cyst content of the soil was almost solely confined to the surface soil. No deep ploughing had been done in either field for many years and a very short distance below the surface the laminated appearance characteristic of unbroken "warp" land could be clearly seen. From the 16 acre field forty numbered samples of surface soil were taken with a trowel. The position from which each sample was taken was marked on a scale map at the time in order that future samples might be taken from approximately the same places, thus ensuring that irregularities in the cyst content of the soil should not confuse the results. Only one-half of the control field was sampled and fewer samples were taken in this case.

Cyst counts per 200 grammes of soil were made from each sample, and fifty cysts were dissected from each sample from the experimental field, one hundred from each from the control field. Viable contents estimations were then carried out by the method described above. From the almost triangular experimental field the samples were taken in four rows, and the first and longest row was found to be the most heavily infected, the intensity of infection dwindling towards the opposite corner from which the last row of only four samples was taken. In eight instances less than fifty cysts were obtained from the soil sample and in these cases estimations were not made.

The percentage viable contents of the cysts on the three occasions when estimations have been carried out are tabulated in detail for each of the four rows, below. On the first occasion, before the grasses had been sown, the viable contents of the cysts from the field as a whole were found

to be 70·92% of the possible maximum. In the control field the percentage was slightly less, viz., 68·75% of the possible maximum.

The seeds mixture used in the experimental field was as follows :—16 lbs. Kentish indigenous rye grass, 6 lbs. smooth stalked meadow grass, 1 lb. wild white clover per acre. This mixture was considered to be suitable to the type of soil, likely to become easily established under suitable weather conditions following spring sowing, and calculated to yield a reasonably good hay crop. The clover, which was known to be without stimulant effect on the nematodes, was included solely for this last purpose as it was intended to conduct the experiment upon the most practical lines possible from the economic point of view. This seeds mixture was sown on the experimental field in April 1931, the winter wheat being left as a useful cover crop.

In September 1931, after the harvesting of the wheat, soil samples were again taken from the same points in both fields. The grasses and clover were found to have become well established in the experimental field and an exhaustive examination of the roots failed to reveal any trace of nematode infection. Estimations of the viable contents of the cysts from this second series of samples showed that in the experimental field the unhatched eggs remaining in the cysts were now only 54·42% of the possible maximum egg content. That is to say, the viable contents of the cysts had been reduced, between April and September, by 23·27% (previously erroneously quoted as 23·6%).

The reduction in the control field was found to be rather surprisingly low, being only 1·92% of the original finding. A comparison of the detailed figures obtained during the course of the estimations gave some indication, however, of the probable cause of this low figure, for whereas in the experimental field the number of empty and partially full cysts had increased in each case, the full cysts alone being reduced in number, in the control field a marked decrease in the number of empty cysts was shown. This may be attributed to the break-up of empty cysts in the soil, a process which must be continually taking place, but whereas in the experimental field fresh cysts were constantly being emptied to replace those which became broken up, this replacement did not take place in the control field. This explanation, if correct, would seem to indicate a grave

defect in the method adopted in comparing the viable cyst contents of soils.

During the following year, 1932, the grass ley in the experimental field yielded a fair crop of hay. The control field should have been sown with the usual grass mixture suitable for a one-year ley which was commonly included in the rotation. This mixture contained a proportion of rye grass but no meadow grass. Unfortunately a mixture almost identical with that used in the experiment was substituted by the grower so that as a control for the experiment this field was rendered useless.

A third series of soil samples was taken from both fields in September 1932 and estimations of cyst contents were carried out as on the previous occasions. In the experimental field the percentage of residual viable contents was found to have fallen during the year from 54·42% to 36·43% of the possible maximum. That is, a reduction of 33·05% in the eelworm infection had been produced in twelve months, or by comparison with the original samples taken before the treatment was begun, the infection had been reduced in the field as a whole by 48·63% within eighteen months.

In the control field the infection was found to have been reduced by 24·7% following the sowing of the grass mixture. This is of interest in that it corresponds very closely with the first year's result of the grass mixture in the experimental field.

The experiment is being continued throughout the present season and the remaining eelworm infection will be estimated this autumn. Two other infected fields which had been cropped with potatoes in 1930 and are undergoing a rotation of cereal crops were sampled in September 1932 with a view to serving as controls for the 1933 results, but in both cases the cyst content of the soil and the viable egg content of the cysts was found to be much lower than had been the case in the two original fields chosen ; it is therefore not anticipated that these will form a very satisfactory standard for comparison. Meanwhile a field experiment on similar lines has been begun in Bedfordshire.

Discussion.

The reduction in the viable contents of the cysts in the experimental field has been relatively consistent throughout, as is shown by the tabulated results of the findings up to September 1932, where each portion of the field is dealt with separately. The figure indicative of the reduction in eelworm

content of the field as a whole, viz., 48·63% of the original eelworm content, in only eighteen months, seems sufficiently striking to render the loss of the control doubly unfortunate. The second year's result obtained from the control field is, however, not without value in that it corroborates the first season's result in the original experiment.

TABLE OF CYST CONTENTS FROM EXPERIMENTAL FIELD ON THREE OCCASIONS OF SAMPLING.

Row of sampling.	Date.	Full cysts %	Empty cysts %	Three-quarter-full cysts %	Half-full cysts %	Quarter-full cysts %
Row 1 16 samples	Jan. 1931	71·68	19·75	4·75	3·33	2·0
	Sept. 1931	43·7	27·43	17·0	8·0	3·87
	Sept. 1932	28·8	42·4	11·4	8·4	9·0
Row 2 12 samples	Jan. 1931	63·6	21·8	7·0	4·0	3·3
	Sept. 1931	39·3	32·0	15·16	6·84	6·6
	Sept. 1932	20·8	47·0	13·4	8·4	10·4
Row 3 8 samples	Jan. 1931	59·8	28·5	3·6	4·0	4·0
	Sept. 1931	26·57	47·9	12·7	4·85	8·0
	Sept. 1932	10·75	63·25	11·1	6·0	8·9
Row 4 4 samples	Jan. 1931	43·3	42·3	8·0	4·3	2·7
	Sept. 1931	34·5	44·5	11·0	5·5	4·5
	Sept. 1932	8·0	58·5	18·75	6·25	8·5

It is hoped to devise some means of estimating the viable eelworm content of soil which will reduce the margin of probable error, which, it is realised, must be very considerable in the method in use up to date.

An important aspect of the researches on this method of eelworm eradication which has not so far been mentioned, is that, at the present stage of the work, no information is available on the effects of the treatment on the disease known as "potato sickness" in the production of which eelworm is one of two or more factors. Although "potato sickness" occurs only

on land where the nematode is present, it is an established fact that some contributory condition of the soil which is not at present understood must be present for the symptoms of " potato sickness " to arise. Whether this condition is in any way affected by the grasses is not known, but any effect they may have is as likely to be detrimental as advantageous. In this connection it should be noted that disease symptoms occur chiefly where potatoes are grown continuously for many years on the same land. This suggests that a second factor in the production of the disease may be associated with accumulations of root excretions, or their breakdown products in the soil, and, since the root excretions ot the grasses used must in some way resemble those of the potato, the cultivation for several years of these grasses may, while eliminating one cause of disease, merely aggravate another. Until the experiments which are in progress to elucidate this and other problems which arise in connection with the work have been satisfactorily concluded the economic value of the results so far obtained remains obscure.

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A Dwarfing Disease of Cultivated Violets associated with the Eelworm, *Aphelenchoides olesistus*.

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INTRODUCTION.

MORE than twenty years ago Schwartz (1911) described a disease of cultivated violets associated with eelworm attack. The plants were obtained from gardens at Greiz and Kreuznach in Germany and in all cases had distinct gall-like swellings at the bases of the leaf-stalks. As the disease progressed the leaves became smaller and smaller and the leaf-stalks shorter until, finally, an irregular, walnut-sized gall was produced the surface of which was covered with abortive buds. Schwartz drew attention to the similarity presented by such plants to the "cauliflower" condition in strawberry plants associated with the presence of *Aphelenchoides fragariae*. Goffart (1930) mentioned the fact that the disease persisted for a time in Germany; being reported in 1910-12 and 1915-17 but had not been recorded again up to 1930.

The nematode parasites found by Schwartz were classified by him as a variety of *Aphelenchoides olesistus* namely, var. *longicollis*. In England the only previous record we have been able to find of diseases in cultivated violets associated with eelworm attack is one by Hodson who in 1924 reported *A. olesistus* var. *longicollis* from plants in Devon; the particular variety affected being *Mrs. Lloyd George*. Although Hodson gave the nematodes Schwartz's varietal name, *longicollis*, he has informed us personally that there was no gall-formation on the affected plants and it is highly probable that he encountered the type of damage dealt with in the present paper.

Two important points of difference may be noted here between the disease of violets described by Schwartz and that now occurring in Devon. 1. The German plants exhibited marked gall-formation whereas no galls have been found on the violets suffering from the present disease. 2. The nematodes were endoparasitic in the galls found by Schwartz whilst in the case of the violets from Devon they are entirely ectoparasitic in habit. Another difference is that the parasites we have studied belong to the species *Aphelenchoides olesistus* and not to its variety *longicollis*.

The purpose of the present paper is to put on record the occurrence of the disease, its incidence and symptoms, together with an account of the nematodes invariably present on affected plants and suggested methods of control.

Incidence of the Disease.

The dwarfing trouble was first brought to the notice of one of us (L. N. S.) during early September 1932 by a grower in the Dawlish area of South Devon. This grower reported that a small area of plants, about three yards in diameter, in a two year old bed of violets were " very flat and stunted " ; the variety of violet was *Princess of Wales*. The patch of affected plants appeared to the grower to be spreading, but very slowly, and he recalled that in the same part of the field in the previous year, he had noticed a few plants which appeared to be weak but that he had not considered it to be of any importance. An examination of these plants revealed the presence of eelworms which proved to be *Aphelenchoides olesistus*. A careful search through other fields of violets of the same variety, but in another part of the farm some distance away, brought to light a fair number of isolated plants showing similar stunting. In these plants, also, eelworms were found.

The matter was brought to the notice of violet growers in the district and several said that they thought the trouble was present in their violets and also remarked that they had seen such plants for some years, but only in isolated instances. Visits to these growers showed that dwarfed plants were to be found in small numbers on all these farms and that eelworms were present in them. The variety of violet was in all cases, *Princess of Wales*.

Early in November a case of eelworm in another variety, *Kaiser Wilhelm*, occurred in the Newton Abbot district. In this instance the

attack was much more severe, almost half an acre being so severely affected as to produce little or no crop of flowers. The financial loss to the grower was considerable. The area of attacked plants in this case was in the form of a belt running across the field which was also planted with fruit trees; the violets growing beneath the trees. The ground sloped fairly steeply and the conditions were such that it seemed clear

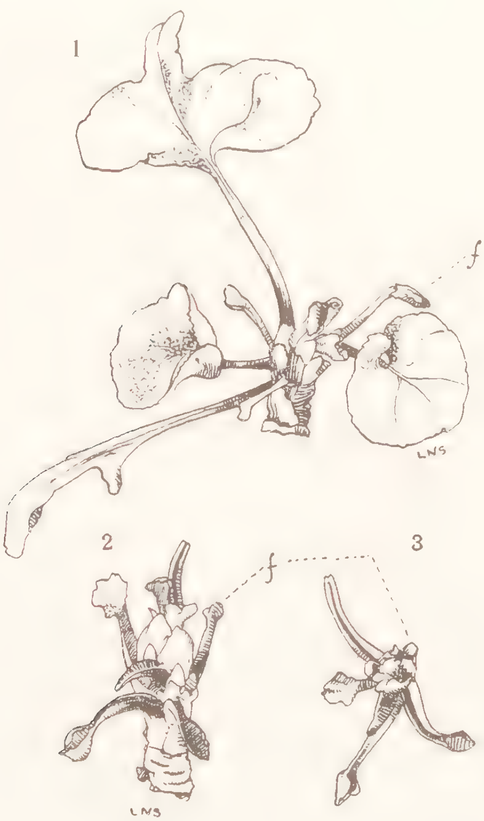


Fig. 1.—Violet plant showing early symptoms of dwarfing disease. *f.* flower bud. Natural size.

Figs. 2 and 3.—Crown of severely diseased violet plant. 2, side view; 3, seen from above. *f.* flower bud. About twice natural size.

that neither shade nor wet conditions at the bottom of the slope were important contributory factors.

Another severe case, in two year old plants of the variety *Princess of Wales*, occurred in the Dawlish area. Here the plants over a circular area of some 10 yards diameter were stunted ; the dwarf condition being accentuated nearer to the centre of the area. The plants on the edge of the area bore runners with the same symptoms ; in the centre the plants were too weak to produce runners.

Subsequent visits to various parts of Devon and Cornwall have shown that the trouble is widespread to varying degrees and it would seem to be an important factor in the gradual decline in the vigour of violets of which many growers are complaining. In addition to *Princess of Wales* and *Kaiser Wilhelm*, dwarfing has also been found in the variety *Mrs. Lloyd George* and in several double varieties. The dwarfing is, on the whole, more marked in two year old plants than in those only one year old.

Symptoms.

The symptoms as observed since the first appearance of dwarfed plants at Dawlish may be summarised as follows :—Dwarf plants have a generally stunted and flattened appearance when all the crowns are affected. It is frequently found, however, that only a proportion of the crowns on a plant exhibit the symptoms, the remaining crowns being apparently healthy. Individual crowns exhibit the symptoms in varying degrees. In cases where the dwarfing is slight, the outer leaves are often normal in appearance, the inner ring of leaves becoming successively smaller and more deformed. The first sign of deformation is that the leaves are not prolonged backwards into lobes typical of healthy leaves, the hinder margin of the leaf on each side tending to be at right angles to the petiole. The margins of the leaves also become successively less markedly toothed, and the degree of hairiness of the leaf surface and of the petiole reduced. Fig. 1 shows such a crown in an early stage of attack. There exists a definite gradation between such lightly attacked crowns and those extremely dwarfed. In these extreme cases seldom more than one healthy leaf is present and this is usually small in size. The whole crown is usually very small and may only stand an inch or less above ground level. The general appearance is remarkably similar to the well-known " red-plant

disease " of strawberries, as found in those varieties where no red colouration occurs, *e.g.*, *Sir Joseph Paxton.* The leaves are successively smaller and smaller in size and may range from as little as half an inch across

Aphelenchoides olesistus.

Figs. 4 and 5.—Adult male and female respectively from diseased violet plant.

Figs. 6 and 7.—Adult female and male respectively from diseased fern.

down to a quarter of an inch. Occasionally no leaf lamina is present, only the petiole being formed. The edges of the leaves become devoid of teeth and their hinder margins may run forward from the petioles with a complete absence of hairs on leaf surfaces and petioles. The latter also curve outwards and downwards; the upper surfaces of the leaves sometimes being presented to the surface of the soil. The petioles also show definite tapering towards the leaf blades.

The symptoms, so far as flowers are concerned, also show differences between slightly and severely affected plants. The appearance of the flowers ranges in the former from flowers with stalks too short for market purposes to complete absence of the latter. In severely attacked crowns the flowers are very small, are borne on very short stalks, and are so deformed that they cannot open. It is only the presence of a certain amount of violet colouration that renders distinction from small deformed leaves possible. Figs. 2 and 3 illustrate a severely attacked crown about twice natural size, viewed from the side and from above. A more or less normal leaf was present but was removed before sketching.

Runners from attacked crowns were observed frequently, but not invariably, to have developed similar symptoms.

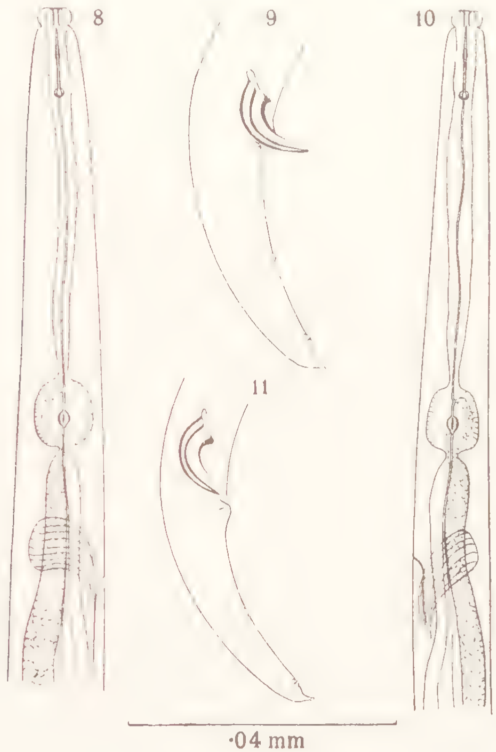
Habitat of the Parasite.

As has already been pointed out in the introduction, the associated eelworms are entirely ectoparasitic in habit. They occur on the crown of the plant amongst the bases of the leaf stalks and developing leaves surrounding the growing point. When these structures are carefully removed and washed by forcibly squirting water on to them from a pipette, the nematodes are found in the washings.

Morphology of the Parasites.

Dimensions:—*female*: length, 0·71 mm. to 0·85 mm.; $\alpha=43–50$, $\beta=10–11$, $\gamma=14–17$, V$=67\%–69\%$. *male*: length, 0·65 mm. to 0·75 mm. $\alpha=44–49$, $\beta=9·6–10·6$, $\gamma=17·5–19·5$, spicules, dorsal pieces, $18\mu–19\mu$, ventral piece, 9μ-10μ. The foregoing dimensions may be compared with the following based on specimens obtained from diseased ferns, *female*: length, 0·57 mm. to 0·76 mm., $\alpha=44–47$, $\beta=10–10·6$, $\gamma=14·7–19$, V$=66\%–68\%$; *male*: length, 0·47 mm. to 0·66 mm., $\alpha=46–50$, $\beta=8–10$, $\gamma=16–20$; spicules, dorsal pieces, $14\mu–16\mu$, ventral piece, $8\mu–9\mu$.

At the time that the eelworms from violets were being studied diseased material of ferns was available and a close comparison between the forms from both host plants was thus possible. We have identified the worms from violets as belonging to the species *Aphelenchoides olesistus* since we can establish no constant morphological differences between them and the



Aphelenchoides olesistus.

Figs. 8 and 9.—Fore part of body and male tail from violet material.

Figs. 10 and 11.—Fore part of body and male tail from fern material.

species causing leaf-blotch in ferns, except one of size ; the nematodes from violets being on the whole larger than those from ferns.

The general anatomy and structure of the adults of *Aphelenchoides olesistus* has been dealt with in an earlier paper by Goodey (1928) and it is therefore unnecessary to describe it in detail here, especially as the accompanying drawings, figs. 4-11, show all that is required. Particular attention was, however, paid to two features—1, the position of the excretory pore relative to the nerve ring and the oesophageal bulb ; 2, the curvature of the male tail on killing by heat since these are of importance in differentiating *A. olesistus* from *A. fragariae* and *A. ritzema-bosi*. As figs. 8 and 11 show, the excretory pore is practically on a level with the nerve ring in worms from both violets and ferns. It was also apparent when worms were killed by heat, that the male tail took on but a slight ventral curvature. These two features, in conjunction with the general shape and size confirmed the identity of the worms as *A. olesistus*.

Schwartz differentiated the variety, *longicollis*, from the species *A. olesistus* on the following structural details—1, the somewhat heavier build of the stylet whose basal swellings were more marked ; 2, the slightly greater length of the oesophagus ; the proportion β, *i.e.*, body length to length of oesophagus, being 9 as compared with 11 in females and 8 as compared with 9 in males ; 3, the greater distance of the excretory pore from the anterior end ; 4, the somewhat larger spicules of the male. It was a matter of interest, therefore, to compare the forms from violets and ferns in respect to these anatomical features. In spite of the fact that the nematodes from violets are slightly larger than those from ferns, it was soon apparent, when a series of drawings was made of the head and oesophageal regions under high magnification, that no differences as regards points 1–3 could be established. The stylet had the same length in each and its basal swellings were no more prominent in the violet forms than in those from ferns. The length of the oesophagus, *i.e.*, the distance of the posterior edge of the muscular bulb from the anterior end of the body, was practically the same for worms from each host. The distance of the excretory pore from the anterior end was also practically the same in all cases. The only difference noted was that the spicules were slightly larger in males from violets than in those from ferns. In view of these considerations it was decided that the nematodes from violets could not be placed in the variety *longicollis* but must belong to the species *A. olesistus*.

Control Measures.

Whilst it has not been possible in the time at the writers' disposal since the discovery of the affected violets to devise definite means of control, the following suggestions may be made, being supported by experiments and observations in the field.

1. Since runners from affected plants are frequently found to be affected, the greatest possible care should be taken to propagate only from healthy, vigorous plants. Any runners showing symptoms must be rejected even if from healthy parents.

2. During the season any plants developing the symptoms should be removed and destroyed.

3. Everything possible should be done to encourage regular growth of the plants.

4. Though there is, as yet, no evidence to suggest that the eelworm may spend any part of its existence in the soil, it is clearly advisable to avoid growing violets on the same ground for two successive seasons.

5. Preliminary experiments in the treatment of runners by immersion in hot water strongly suggest that this may prove a satisfactory means of freeing runners from eelworm prior to planting. In the experiments, healthy, vigorous runners were treated and planted. For comparison with these, other runners lacking in vigour and having dwarf symptoms well developed, were also treated. In each case some of the runners of each class were planted out untreated as controls. The heat treatments were carried out in an electrically heated bulb bath controlled by a thermostat. Two varieties of violet were used, viz., *Princess of Wales* and *Kaiser Wilhelm*. The treatments were carried out on April 4th and immediately following the hot water bath the runners were plunged for a few minutes into cold water in order to cool them rapidly. They were then planted out at once. The weather was hot and dry at the time and no rain fell for some days: in view of these unsuitable conditions the results obtained are very satisfactory. The treatments given were carried out at a temperature of 110°F. for periods of 15, 20 and 30 minutes respectively and at a temperature of 108°F. for 20 and 30 minutes respectively. The best results were obtained when the treatment was carried out at a temperature of 110°F. for 30 minutes. Much of the older leaf present on the runners was killed but new leaves were soon

produced. In the case of the eelworm affected runners the new leaves showed little of the symptoms of attack, but their initial weakness was so great that they did not grow into satisfactory plants.

Briefly, the work so far as it has progressed, suggests that the hot water treatment of runners at a temperature of 110°F. for a period of 30 minutes followed immediately by plunging into cold water, is likely to prove satisfactory. Runners should be planted soon after treatment under good conditions. It would seem that there is little to be gained by treating badly affected runners and careful selection should be carried out to supplement such treatments.

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On the Chrysanthemum Nematode, *Aphelenchoides ritzema-bosi* Schwartz, 1911 and its Control.

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Introduction.

This paper embodies certain experiments on control of the nematode *Aphelenchoides ritzema-bosi* Schwartz, 1911, on chrysanthemums, and were started in September 1930 at the request of several commercial chrysanthemum growers in Staffordshire and Warwickshire.

The disease produced by this nematode, commonly known as the leaf-blotch eelworm disease, has developed in recent years with such alarming rapidity as to threaten the entire chrysanthemum industry. In many nurseries it has already placed the growing of certain varieties of chrysanthemums very largely beyond the power of commercial enterprise. At the moment it is probably not fully realised how serious is the loss caused by *A. ritzema-bosi*, because the damage really due to this eelworm has, it is believed, often been attributed to other causes. The rapid spread of the nematode in recent years is put down mainly to the ease with which infested plants and their cuttings can be transported from one district to another in the ordinary course of this enormously increased commerce. In consequence, the progressive grower, who is anxious to plant new varieties and who buys chrysanthemums freely from both home and foreign sources, is often the first in the locality to suffer from this most devastating of all chrysanthemum pests.

The nematode is now distributed throughout all the principal chrysanthemum growing districts in this country and it also occurs in Sweden, Denmark, Holland, France, Switzerland, Germany, Austria, Czechoslovakia, U.S.A., South Africa, Brazil and Japan.

Brief Review of Previous Work.

The publications on *A. ritzema-bosi* before the present year have been summarised by Goodey in his book on Plant Parasitic Nematodes (1933), so that detailed consideration of this work is not necessary. It is noteworthy, however, that the earliest record of eelworm disease on chrysanthemum leaves in this country is one by an anonymous contributor in the Gardeners' Chronicle for 1890, and that it was recorded by Atkinson (1891) and Ritzema Bos (1891) in the United States of America and Holland respectively, by Osterwalder (1899) in Switzerland, Chifflot (1902) in France, Sorauer (1901) in Germany, and Fulmek (1910) in Austria. All these workers, as well as Marcinowski (1908) and Molz (1909), considered the species as *Aphelenchus olesistus* or *A. ormerodis*. Schwartz (1911) differentiated it from these species and called it *A. ritzema-bosi*. In 1921, Stewart gave a very detailed morphological description of the nematode and named it *Aphelenchus phyllophagus*. Goodey, however, in 1923 concluded that *A. phyllophagus* (Stewart 1921) was a synonym of *A. ritzema-bosi* (Schwartz 1911). More recently our knowledge of its anatomy and biology has been further considerably increased chiefly through the work of Goffart (1930), Steiner (1931), Goodey (1928), Roszypal (1926), Smith (1926), Weber (1926), Staehlin (1931), and Voss (1930). In 1933 Goodey has shown that as a result of recent studies by Steiner, and on grounds of priority the generic name *Aphelenchus* must be changed into *Aphelenchoides*.

Various methods of control have been attempted by several of these investigators. The use of different chemicals as lethal agents has proved unsatisfactory. So also has therapeutic treatment of the plant by the use of poisons in high dilution. Marcinowski (1909), and more recently Goffart (1930) and Voss (1930), have shown that the nematode can be prevented from migrating to the foliage by placing a ring of vaseline, bird lime or tanglefoot, about $\frac{1}{5}$ inch wide, round the stem. Goodey (1933) claims that immersing the aerial parts of rooted cuttings in a water-bath at 122°F. for 5 minutes will free the plants from infection. Since treated cuttings want special care he considers the method to be scarcely practical except in the case of plants which are too valuable to be lost.

Life History and Symptoms of Attack.

According to Stewart (1921), the whole life cycle from egg to egg may be completed in fourteen days when day temperature is not less than 60°F.

The nematodes live endoparasitically within the leaves and have also been found in the buds and outer layers of stems. They travel on the outside of plants in films of moisture caused by dew, rain or overhead watering and enter the tissues through the stomata. The nematodes reach the ground in diseased leaves in which they coil up after the manner of a watch-spring. Goodey (1933) asserts that they can remain viable in dry shrivelled leaves for a period of at least three years.

The most common form of attack is discoloration of the lower leaves which take on a patchy or blotched appearance (Fig. 1), and this may occur at any time during the life of the plant. It is often observed during the propagating period (Fig. 4), but generally it does not appear until August or September when the plants are well established. The time at which the foliage becomes seriously affected bears no relation to the age of the plant but is largely determined by relatively high humidity and the presence of surface films of moisture on the plant. Young plants frequently succumb to the attack but older plants may often be induced to grow away from such attack if suitably stimulated by means of correctly balanced nitrogenous-potassic manures. However, even if plants be saved by this means the bloom is almost invariably inferior to that of healthy plants.

On the leaves the discoloured areas generally first appear at the apex or at the angle formed by two lobes (Figs. 1a, 1b). The lesions begin as pale green spots which soon become brown or black and, usually, in the case of most varieties, have a yellowish peripheral zone (Fig. 1y). The affected parts vary in shape but usually develop into irregular patches, although sometimes these appear as distinct areas between the veins (Fig. 1b). Under suitable atmospheric conditions the blotched areas increase very rapidly in size, two or more often emerging into each other, and in consequence the leaf collapses and dies (Fig. 1d). The leaves nearest the base of the plant are the first attacked but in severe infestation the infection rapidly progresses upwards until finally the whole of the foliage may be attacked, shrivel up, and hang down along the stem (Fig. 6). Dead leaves do not drop off immediately and, as new leaves are not produced to replace them, the infected plants present a gaunt appearance (Fig. 6). As a result of premature defoliation the flower buds remain small and weak and their growth may even be entirely checked.

Often associated with the discoloration and destruction of the foliage and reduction in size of the blossom there is deformation of the leaves and flowers. In such instances, some of the leaves may be almost filiform, greatly reduced in size, or of an abnormal shape, in which event the edges are smooth or with an indentation of an irregular type (Fig. 3). Deformed flowers, besides being undersized, may be found with much thickened and dwarfed stalks and a corolla exhibiting extreme malformation in that the petals are reduced in parts to mere rudiments or even remain undeveloped (Fig. 3). The exact relationship of these leaf and flower deformations to the disease has not yet been discovered.

Severely attacked plants also show, in most cases, a decline in the formation of cuttings and even those produced are often completely destroyed (Fig. 4). This is particularly so when the amount of moisture present is kept above the minimum necessary for the migration of the nematodes to the developing foliage by overhead watering of the plants.

Experiments on Control.

Experiments 1930-31.—It is a fact well known to helminthologists that nematodes are easily killed by heat. Acting on this knowledge, it was decided by the writer in 1930 to carry out some experiments to determine the temperature at which *Aphelenchoides ritzema-bosi* are killed. It was found that 10 minutes at a temperature of 110°F. was lethal to nematodes in water. Large numbers of cuttings of different varieties were then taken from affected chrysanthemums together with equal numbers of cuttings from healthy plants and immersed in water at 110°F. for periods ranging from 1 to 30 minutes. Immediately after treatment the cuttings were planted in pots with steam sterilised soil. A certain number of untreated eelworm-free cuttings from each of the different varieties were also planted. The results obtained in these trials showed clearly that chrysanthemum cuttings, at least unrooted ones, are not able to withstand immersion in water at 110°F. for a time sufficient to control the eelworm.

Experiments 1931–32.—It was decided in 1931 to explore the possibilities of controlling the nematode by subjecting chrysanthemum stools or root stocks in autumn to water at a temperature of 110°F. All the plants (variety " Harvester ") selected for the purpose were known to be heavily infested with the nematode. Before treatment the soil was carefully washed off the underground parts of the plants and the cuttings

were removed. The times of immersion of the stools in water at 110°F. were :—

Series	I	Untreated plants (control).
,,	II	Immersion for 10 minutes.
,,	III	,, 20 ,,
,,	IV	,, 30 ,,
,,	V	,, 45 ,,
,,	VI	,, 1 hour.

Immediately after the hot water treatment, the stools were cooled by means of cold water and planted with as little delay as possible in 9-inch brown earthenware pots filled with soil which had never grown chrysanthemums. The untreated or control stools received the same preparation as the treated ones, being cleaned of all soil and cuttings and replanted in new soil from an uninfected source. The pots with treated and control plants were placed in a heated greenhouse for the production of cuttings. Subsequent examinations revealed that chrysanthemum stools, at least those of the variety "Harvester," are able to withstand immersion in water at 110°F. up to one hour but that the longer exposures had a very marked effect both on growth and number of cuttings produced. Immersions of 10 and 20 minutes duration retarded the production of cuttings for nearly 7 and 14 days respectively, and those of 30 and 45 minutes for three to four weeks. The appearance of the plants during the third week in February, that is nine weeks after treatment of the stools is reproduced in Fig. 2. The pot marked A was from Series I, in which untreated stools had been used ; those marked B, C, and D from Series II, III and IV, in which plants immersed in water for 10, 20 and 30 minutes, respectively, had been used. The average length of the cuttings two months after treatment of the stools were :—

Series	I	Untreated plants	6″	approx.
,,	II	Stools immersed for 10 mins.	4″	,,
,,	III	,, ,, 20 ,,	3″	,,
,,	IV	,, ,, 30 ,,	2″	,,
,,	V	,, ,, 45 ,,	1½″	,,
,,	VI	,, ,, 60 ,,	½″	,,

There was also a marked difference in the number of cuttings produced under the various treatments as compared with the control plants. Plants in Series II and III produced the highest number of cuttings, those in Series VI the least, whilst those in Series IV and V were intermediate

in this respect. The number of cuttings in Series II and III, though somewhat reduced, was considered fairly satisfactory from the practical standpoint.

Several cuttings were taken from each of the control and treated stools during the third week of February and planted in pots of soil which had not previously been used for chrysanthemums. These cuttings were kept in a heated greenhouse and grown in such a way as to approach as closely as possible the conditions in commercial cultivation of chrysanthemums. All made a satisfactory growth and were transplanted into their final pots in the latter part of May when they were placed in wire-covered enclosures in the open air, and thus exposed until the bloom was cut and the final examination for the presence of the nematode made.

Very little difference could be detected throughout the growing season in the appearance of the cuttings except in the advancement of growth of those obtained from untreated stock plants (Series I). In this case, flower buds appeared about eight days in advance of the others. Slight differences were also apparent in the earlier part of the season between the plants obtained from the treated stools (Series II–VI). As the season progressed these differences became less and less marked until ultimately the plants were undistinguishable as regards growth.

All the plants remained free from the nematode attack till about the beginning of September. On September 30th and subsequent days a careful examination of the individual plants was made and the intensity of infection noted. This examination showed that all the plants derived from the control stools (Series I) were infected, as well as those from stools immersed in water at 110°F. for 10 minutes. The plants obtained from stools which had been dipped for 30 minutes or over (Series IV, V, VI) remained entirely free from attack throughout the season whilst 60 per cent. of those from stools immersed for 20 minutes were found infected (Series III). There was also a marked difference in the intensity of infestation under the various treatments (Series I, II and III) as judged by the number of leaves attacked. The system of marking employed for assessing the degree of infestation was to judge each individual plant, 10 marks being given where the number of leaves attacked was severe, with graduations down to 0 where the damage was negligible. An average of approximately 4 was recorded in this way for the infected plants derived

from stools immersed for 20 minutes (Series III), 6 for those from stools treated for 10 minutes (Series II) and 8 for the controls (Series I).

This experiment taken by itself strongly suggests that control of *Aphelenchoides ritzema-bosi* can be obtained by submitting chrysanthemum stools, in autumn and before cuttings are taken, to water at 110°F. for a period of not less than 30 minutes. It appears, however, that the adoption of such method would demand special attention to the stools in autumn, particularly in the case of early flowering varieties, to compensate for the retardation in the appearance of cuttings.

Experiments 1932-33.—The object of these experiments was (*a*) to verify the 1931–32 results which strongly indicated that hot water treatment of chrysanthemum stools in the autumn is effective in controlling the nematode, (*b*) to test the effect of longer exposures in hot water than those previously employed, and (*c*) to ascertain whether the retardation effect following the hot water immersion could be overcome by carrying out the treatment when the cuttings are ready to be taken. The chrysanthemum plants used in this experiment were of the variety " Terra Cotta " and part of a stock grown in a commercial nursery in South Warwickshire and which had been a complete failure as a result of a heavy infestation by *A. ritzema-bosi*. A microscopic examination was made of all the plants chosen and only those actually found infected with the eelworm were included in the experiment. The hot water treatment of the stools was carried out during the third week in January and at this time the majority of their cuttings were about 3½ inches in height. The periods of immersion tested were :—

Series	I	Untreated plants (control).	
,,	II	Immersion for	5 minutes
,,	III	,,	10 ,,
,,	IV	,,	15 ,,
,,	V	,,	20 ,,
,,	VI	,,	30 ,,
,,	VII	,,	45 ,,
,,	VIII	,,	1 hour
,,	IX	,,	1½ hours
,,	X	,,	2 ,,
,,	XI	,,	2½ ,,
,,	XII	,,	3 ,,

Immediately after treatment the stools were cooled by cold water and planted in parasite-free soil. An examination of the stools 24 hours after

treatment revealed that the cuttings in Series II, III and IV were vigorous and of a healthy colour ; those in Series V and VI contained few withered leaves ; those in Series VII and VIII had suffered severely, for most of the foliage was shrivelled up and dead ; those in Series IX, X, XI and XII had been completely destroyed. A further examination two days later showed that the cuttings on the stools in Series VII and VIII had also died off.

Cuttings were taken on the third day after treatment off each stool in Series I–VI and grown under the same conditions as those in the 1931-32 experiments. All the cuttings obtained from the stools in Series II, III and IV rooted well and made a normal growth as compared with the cuttings from the control stools (Series I). The cuttings derived from the stools in Series V, on the other hand, were definitely slower in rooting and as a consequence their state of growth throughout the season was somewhat less advanced than that of the cuttings from the stools in Series I–IV. The majority of the cuttings from the stools in Series VI although they retained a healthy appearance for a time ultimately collapsed and died off without striking roots.

In the course of further examination made during the growing season it was found that 33% of the stools in Series VIII and all in Series IX–XII had been destroyed by the treatment, while all the stools in Series II–VII were not adversely affected.

Approximately seven weeks from the date of the hot water treatment, cuttings were again taken from the stools in Series VI and VII and from the remaining ones in Series VIII, since the first cuttings taken in these three series, as already explained, had failed to grow. All these later cuttings (Series VI–VIII) made a rapid growth but were throughout the season decidedly less advanced than those taken earlier in the year from stools in Series I–V.

In May all the cuttings (Series I–VIII) were transplanted into their final pots, which were then plunged in groups in a bed of ashes and soil in an open air wire-covered enclosure, where they remained until the third week in September. They were afterwards kept in a heated greenhouse.

Judging from observations made on the incidence of *A. ritzema-bosi* on the plants derived from the control Series (Series I) together with those made in a large number of commercial chrysanthemum nurseries in

Staffordshire and Warwickshire, 1933 appeared to be very unfavourable to the increase of this nematode. The attack on the controls (Series I) though general was only of a moderate intensity and had little effect on the plants except in considerable destruction of the foliage late in the season (Fig. 5). The plants obtained from stools in Series II were equally heavily infested, but the plants from those in Series III showed much improvement in this respect, as compared with the controls. The plants obtained from stools in Series IV–VIII, on the other hand, apparently remained free of infection throughout the season.

The comparative appearance, towards the middle of October, of the plants in Series I and IV is shown on Fig. 5. The pot marked A was from the Control Series (Series I) and that marked D was from Series IV in which stools immersed for 15 minutes had been used.

These 1932-33 experiments give further indications of the value of the hot water treatment of chrysanthemum stools against *Aphelenchoides ritzema-bosi* and are in general agreement with those of 1931-32. In view of the results obtained in these later experiments, it appears that the retardation in growth produced by submitting the stools to water at 110°F. can be overcome provided the treatment is carried out when the cuttings are ready to be taken and the duration of the immersion is 15 minutes. It must be emphasized, however, that these experiments are to be regarded as preliminary ones, and further extensive trials must be conducted over several seasons before final conclusions can be reached.

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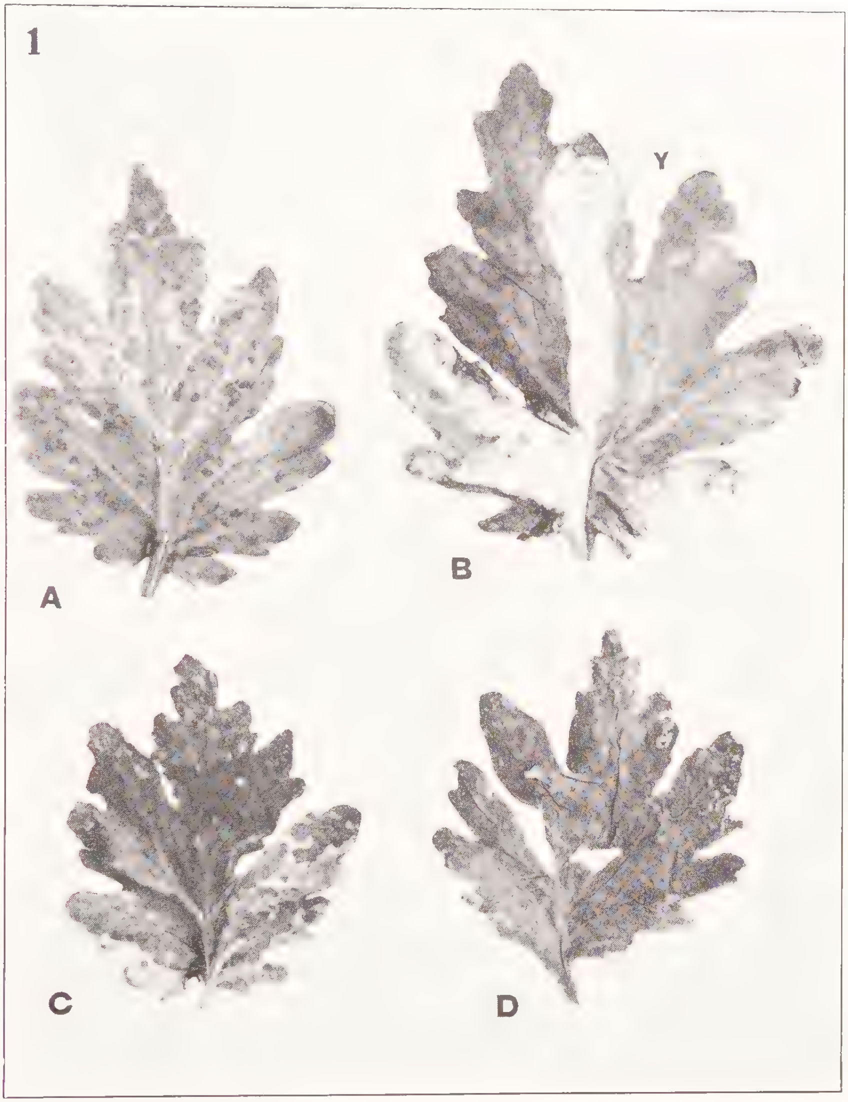

Fig. 1.—Chrysanthemum leaves showing varying degrees of disease condition due to attack by *A. ritzema-bosi.*

(To face Page 32.)

Fig. 2.—Comparative appearance of cuttings in the control and certain treated series in the 1931-32 experiments.

Fig. 3.—Illustrates certain chrysanthemum foliage and flower malformations which are often associated with heavy *A. ritzema-bosi* attacks.

Fig. 4.—Typical example of Chrysanthemum cuttings completely destroyed in the propagating period by *A. ritzema-bosi*.

Fig. 5.—Typical chrysanthemum plant from the control (A) and from one of the treated series (D) in the 1932-33 experiments.

Figs. 6 and 7.—Chrysanthemums showing progressive symptoms of infestation by *A. ritzema-bosi*.

1 3

2 4

Effects of *Anguillulina dipsaci* on Iris

Figs. 1 and 2.—Dutch bulbs with almost entire absence of external symptoms but a ring-like attack internally.

Figs. 3 and 4.—English bulbs with surface damage but more localised internal attack.

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Anguillulina dipsaci (Kühn), as a pest of Bulbous Irises.

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It is only within the last few years that the various species of Bulbous Irises have been recognised as host of *Anguillulina dipsaci*. Despite the comparative paucity of information on the matter there is evidence of the likelihood of infestations becoming serious in the immediate future. It may, therefore, be of value to place on record such information as is at present available.

Historical.

In 1925 Ritzema Bos recorded the occurrence of *A. dipsaci* in bulbous iris in Holland, and in 1926 made further reference to the subject. Goodey in 1929 includes Spanish iris, *Iris Xiphium* in his list of host plants of the nematode. In an American list published in 1932 Steiner & Buhrer include both *I. Xiphium* and English iris, *I. Xiphioides*. Finally, Steiner & Buhrer in a note published in January 1933 give a brief account of the occurrence in U.S.A. from 1928, in which year it was first found there, until 1932. Further reference will be made to this publication, and it is of interest to note that the nematode was reported as being found in all four species or hybrids general in commerce, viz., *I. Xiphium, I. Xiphioides*, Dutch iris, *I. Xiphium*, hybrid, and the Morocco iris, *I. Tingitana*. Of the total of 38 infested samples detected 15 were American grown bulbs, and the remainder bulbs imported from England, Canada, France and Holland.

Occurrence in England.

Not until the autumn of 1932 was the occurrence noted in England, when infested samples of English Iris, *I. Xiphioides*, were submitted both to Goodey and the writer. Both samples emanated from the same source, and the bulbs had been purchased from Holland in the previous year. As an outcome of this record the writer, during the late autumn of 1932,

examined numerous samples of iris bulbs obtained from a variety of sources. At this time *A. dipsaci* could not be detected in any samples other than in *I. Xiphioides.* In this species a surprisingly high incidence of infection was disclosed. Many of the bulbs sampled definitely came from Holland, and it is probable that the great majority of those whose history was unprocurable also did so. Named varieties infected included Sky Blue, Blue King and Bridesmaid, and in all no less than 9 samples out of a total of 24 examined were infested. At about this time a Dutch bulb exporter informed the writer that the amazing incidence of the eelworm in English Iris in Holland since 1930 was causing much concern amongst the growers in that country. It must be stated that this observation was not entirely borne out by those of the writer who, during a visit to Holland in June 1933 was enabled, by the courtesy of Professor van Slogteren, to visit many of the principal growers of English and other Iris. Nematode infection was certainly not unknown, but field examinations showed it to be less common than was suggested by the state of Dutch stocks exposed for sale in England in the previous autumn.

Records of *A. dipsaci* attacking species of iris other than *I. Xiphioides* are in England meagre, very possibly merely on account of their having been overlooked. In December 1932 the writer found the variety Wedgewood attacked, again the bulbs being of Dutch origin. This record is of importance in that Wedgewood is a distinct hybrid and is not included as a host in the American or other literature. The symptoms of attack were identical with those shortly to be described for *I. Xiphioides.*

Finally, in May 1933 a large stock of *I. Xiphium* hybrid, var. Imperator was found to be infected. This stock had been in the ground in England for 3 years although originally purchased from Holland. As the symptoms of attack differ materially from those observed in *I. Xiphioides* they will, in due course, be described separately.

Symptoms of Attack in *I. Xiphioides.*

(*a*) *In the dormant bulb.*

Steiner and Buhrer have briefly described the symptoms of attack as observed in U.S.A., the account being a generalised one of the symptoms commonly observed in bulbous iris regardless of variety or species. This description can be somewhat amplified as a result of the writer's observations.

In *I. Xiphioides* infection is hard to detect in the dormant bulbs unless the dried outer bulb scales are first removed. This applies only to the degree of infection, commonly found, for in very heavily attacked bulbs distortion and softness are obvious. Normally the outermost fleshy scales show definite signs of attack. Brownish or yellow lesions are visible on these scales, the lesions being first yellow, becoming brown and raised, and finally sinking inwards and darkening in colour as the attack progresses. Eventually the whole bulb becomes involved and goes into a soft rot. Before the final stage is reached it is usual for the basal region of the bulb to break away from the remainder (as in narcissus). Frequently the base of a bulb may be heavily attacked and the upper portions remain free. Often the attack obviously commenced at the extreme tip of the bulb when it is difficult to detect until far advanced, for the inner scales are first demolished. Often entry may be directly into the side of the bulb, as evinced by the presence of purely local infections, both tip and base of bulb remaining free.

(*b*) *In the field.*

During the summer of 1933 opportunity was made to observe attack in the field, both in England and in Holland. Superficially an attack is fairly obvious, it being characteristic that numerous bulbs show no top growth whatever. Others grow but poorly, foliage being unhealthy in colour, dwarfed and frequently growing at an angle instead of vertically. Foliage removed from definitely infested bulbs was examined on frequent occasions, but no nematodes could be found therein. No galls were found on leaf or flower stems, the attack invariably being entirely confined to the bulbs. Infested bulbs dug up and examined during the growing season showed the typical yellow and brown lesions in the scales, heavily infested by nematodes. In almost every case the base plates were dead or moribund with the resultant absent or very poor root system. Rather surprisingly it was found that frequently quite badly attacked bulbs gave rise to comparatively large new bulbs. A bulb already attacked at planting time is certainly completely destroyed during the ensuing season. Nevertheless, unless the initial attack is very severe it is able first to throw vigorous offspring. Many of these latter are invaded by greater or lesser numbers of nematodes from the soil, prior to their being dug; many survive until the season following and so perpetuate the attack.

Symptoms of Attack in *I. Xiphium* Hybrid.

(*a*) *In the dormant bulb.*

As already stated only in one case has such an attack, in var. Imperator, been observed in England, and it may well be that this is by no means a typical one. At the same time there are features which are worthy of description. In the dormant bulb no surface lesions, so typical of attack in *I. Xiphioides*, could be found, nor was it typical for the bulbs to develop into a soft rot. On cutting through an infested bulb horizontally typical rings of discoloured tissue, from which *A. dipsaci* could be obtained in quantity, were disclosed. In other words the appearance was strikingly reminiscent of that of an attacked narcissus bulb. Infested bulbs kept under observation indicated that the attack progressed very slowly, and a constant feature was the presence of infestation in the extreme tip of the bulbs.

(*b*) *In the field.*

The stock of Imperator bulbs in which the attack was observed were part of a block of 500,000 irises planted in the open in the autumn of 1930, the bulbs coming from Holland. From all accounts growth in 1931 was entirely satisfactory, but in the Spring of 1932 small patches were observed in the field, bulbs within the patches making no top growth whatever. Despite this, hard and, as far as could be seen externally, healthy bulbs were present below ground within the areas in which growth had failed. A similar state of affairs was apparent in the Spring of 1933, when the writer's attention was first drawn to the matter, except that the areas in which the bulbs had failed were, from all accounts, considerably larger than in the previous season. On the periphery of the patches a few bulbs were found which had made poor top growth, but as a general rule a bulb either grew normally or not at all. An examination of bulbs removed from the soil disclosed symptoms similar to those just described. It seems clear that the singular slowness with which the attack progressed within the individual bulb accounted for its continued existence in the soil, whilst the fact that the tip was almost invariably the initial seat of infection might account for the entire absence of top growth. Careful examination failed to disclose any trace of nematode invasion of leaf or flower stem.

It may be that the strain of *A. dipsaci* responsible for this attack is actually a narcissus one. Narcissi attacked by *A. dipsaci* had occupied the land previously, and the method of attack as observed is unlike that normally associated with iris. Experiments in progress should shed further light on this point in due course.

Transmission Experiments with *I. Xiphioides*.

Iris in commercial practice frequently follows narcissus as a crop, it is therefore of importance to ascertain to what extent *A. dipsaci* is likely to transfer from the one to the other. Steiner and Buhrer attempted, without success, to transfer the nematode from bulbous iris to both narcissus and onion. The experiments were small scale ones carried out under glasshouse conditions. The writer has during 1932-33 attempted to transfer 4 *I. Xiphioides* inhabiting strains to narcissus, with entirely negative results. In every case the narcissi employed were of the variety Emperor, which is highly susceptible to attack by *A. dipsaci*. The narcissus had been grown under observation for 2 years and was apparently clean, but as an additional precaution the bulbs were in the autumn of 1932 subjected to a 3-hour hot water treatment at 110°F. Two series of experiments were carried out, each with 4 strains of the nematode occurring in *I. Xiphioides*.

In the first series infected iris bulbs were interplanted with the narcissus Emperor in October 1932. The bulbs were kept under observation throughout the growing season. The iris, without exception, made poor growth and the foliage died prematurely; the Emperor grew normally. Foliage was examined periodically for the presence of nematodes, but in no instance was *A. dipsaci* found therein. All the bulbs were dug and examined during the first week in September 1933. Most of the original iris bulbs were dead, a few new bulbs had developed, and in many of these infestations were present. In no case was there any sign of attack in the Emperor bulbs and no living nematodes were to be found in them.

The second series of experiments were made with a view to testing the ability of the nematodes to enter an alien host in the absence of the preferred one. The technique employed was similar to that previously described by the writer (2). Infected iris bulbs were cut into small pieces, dried, incorporated with soil and the whole used as a top dressing for established Emperor bulbs. The dressings were given twice, in November

1932 and March 1933 respectively, and the Emperor bulbs were lifted and examined early in September. In no case had a typical nematode attack been initiated although a few living *A. dipsaci* were recovered from the neck regions of some of the bulbs. This phenomenon was not unexpected in the light of previous work on similar lines.

Both series of experiments suggest that the strains of *A. dipsaci* inhabiting *I. Xiphioides* are unable to attack also the narcissus.

Control Measures in Iris.

Very little information is at the moment available on this score. Steiner and Buhrer report inconclusive results with hot water treatment of the bulbs, stating that "the effect upon the iris plant itself has not been satisfactory." This observation is entirely borne out by a few preliminary experiments by the writer.

Samples of infested iris were subjected to 1 hour and 2 hour treatment at 110°F. in December 1932. The 1 hour treatment killed all the nematodes within the bulbs, but by March 1933 all treated bulbs were dead. It may be that the season of treatment was quite unsuitable. At the same time, in the light of the resistance shown to such treatment and latitude available as regards time of year at which it is employed, in the case of the narcissus it would appear that this method is likely to prove useless for iris bulbs.

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Helminth Parasites observed in a Herd of Goats maintained at St. Albans, England.

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Introduction.

The question of helminth parasitism in British goats appears to have had little or no attention paid to it. This is somewhat surprising when one considers the fairly large number of goats which must be present in this country and, although no annual statistics as to the number of goats in Britain are available, Holmes Pegler (1929) observes that early in 1925 the Ministry of Agriculture, assisted by the British Goat Society, obtained returns of the number of goats in England and Wales which was set down as, roughly, 60,000. Similarly little definite data is available on the frequency and intensity with which these animals are infected by helminths in different localities. In this paper an attempt is made to supplement the meagre data relative to these conditions.

Since it is a well-known fact that several helminth parasites are common to both sheep and goats it has been found advantageous on several occasions to make use of goats, at the Institute of Agricultural Parasitology, for the purposes of studying the parasites of one or other or both kinds of animals. This has resulted in the building up of a fair sized herd of goats at Winches Farm, the Field Station of the Institute, during the last seven or eight years. While some of the animals have been bred on the Farm many others have been presented as kids, through the kindly co-operation of members of the British Goat Society and others interested in goat rearing, in order to further research work on the parasites of these animals. A very few were purchased either as

breeding nannies or stud goats. For each animal, records, *inter alia*, of date of birth and of the part of the country from which it was sent, in the case of donated goats, were kept. As is natural, some of the animals have died from time to time and in most cases they were examined *post mortem* and the findings, including the presence of helminth parasites, carefully recorded. It has been considered that data relative to the species of helminths found in animals at autopsy should be placed on record to give an indication, not only of the helminth species present in British goats, but also their frequency of occurrence and intensity of infestation.

It should be pointed out here that one of us (Morgan, 1930) recorded the helminths found in 36 goats which had died over a period of two years at the Institute's Farm although it was stated that the number of goats examined was too small for opinion as to the relative frequency of the different species in this country to be formed. The study of the species recorded in this paper is based on *post mortem* examinations of 80 British goats which have died during the past seven years. It should be borne in mind, however, that this number includes the 36 animals referred to above.

Of the 80 goats examined, 14 were entirely free from helminthic infestation. Their ages, at death, ranged from 18 days to 32 weeks and they included 10 animals, from various parts of England, which had been presented to the Institute, 2 animals bred on the Farm and 2 about which no definite information is known although it is probable they were either presented or bought.

The remainder, 66 in number, were all found to harbour worms and their ages, at death, varied from 7 weeks to 7 years. They comprised 33 donated animals, 23 which had been bred on the Farm and 10 presumably presented or bought but concerning which definite information is lacking.

The total number of species found in the animals amounts to 19 and comprises 2 Cestode and 17 Nematode forms. No Trematodes were recovered from any of the goats examined.

CESTODES.

Cysticercus tenuicollis, the larval form of *Taenia hydatigena* Pallas, 1766 in carnivores, was present in 7 animals. These bladder worms

occurred in the peritoneum in small numbers, 3 being the maximum recorded from one animal.

The other Cestode form encountered was *Moniezia* sp. in 4 goats. All the specimens obtained were probably *Moniezia cxpansa* (Rudolphi, 1810). Each of two animals harboured 1 worm, a third animal had 4 specimens and the fourth goat 12 worms in the intestine.

NEMATODES.

Parasites of the Respiratory System.

Dictyocaulus filaria (Rudolphi, 1809), the cause of verminous bronchitis a condition which often terminates fatally, was encountered on one occasion only in a 6 months old kid whose death was apparently hastened by infestation with this lungworm.

Muellerius capillaris (Müller, 1889), on the other hand, occurred more frequently and was found in 14 animals. It is noted by Cameron (1933) as being the commonest lung parasite of goats and sheep in Britain without, however, causing any serious symptoms unless in heavy infections. Of the parasitized goats, 10 had light, 1 a moderately heavy and 3 very heavy infections.

Parasites of the Alimentary Tract.

(*a*) ABOMASUM OR FOURTH STOMACH :

Haemonchus contortus (Rudolphi, 1803), the well-known "stomach-worm" of ruminants, was present in 24 of the animals examined. About half the cases were light infestations, the goats harbouring from 1 up to 25 worms. Five cases were reported as having moderately heavy infections of from 25 to 100 worms, while 4 animals showed heavy infections of well over 100 parasites per animal. This parasite frequently causes a fatal form of gastritis when present in large numbers as well as anaemia due to piercing the mucous membrane of the stomach and feeding upon the blood. In some of the more heavily infected animals death was partly due to gastritis caused by this stomach worm.

Ostertagia circumcincta (Stadelmann, 1894), another causal agent of parasitic gastritis, was recovered from 33 or exactly half the number of goats from which worms were taken. Light infections were recorded for 14 of the animals, 13 had moderately heavy to heavy infections and in the remaining 5 goats the records show very heavy infections.

Ostertagia trifurcata Ransom, 1907, on the other hand, was much more rare in occurrence and was observed as light infections in 2 animals and as a heavy infection in only 1 goat.

Trichostrongylus axei (Cobbold, 1879) [= *extenuatus* (Railliet, 1898)], a parasite in both ruminants and equines, was the final form to be recorded from the fourth stomach. It occurred in 12 animals and the intensity of infection was light in 4, moderately heavy to heavy in 5 and very heavy in 3 cases.

(*b*) SMALL INTESTINE :

Cooperia curticei (Railliet, 1893) was encountered as a light infection in only 1 of the goats.

Nematodirus filicollis (Rudolphi, 1802), another Trichostrongyle, was not very common and was met with in 8 animals. In no case was the infection heavy or very heavy, the records showing 7 cases of light infections and one, moderately heavy.

Trichostrongylus capricola Ransom, 1907. Amongst the members of the genus *Trichostrongylus* this species appears to have been reported from goats only within recent times in this country. Although Nagaty (1930) claims to be the first to record *T. capricola* from British goats, his material coming from a mixed collection of *Trichostrongylus* spp. taken from a kid born in England, actually it had been previously encountered by one of us (Morgan, 1930) in a 7 years old goat which was examined, at death, in May 1929. Since this date 12 other cases of infection with this species have been recorded. Three cases each of light and moderately heavy to heavy infections were noted and in as many as 7 animals records exhibit the fact that the worm occurred in large numbers.

Trichostrongylus colubriformis (Giles, 1892) [= *instabilis* (Railliet, 1893)] was harboured, like *T. capricola*, by 13 animals but in more intense infestations. Three goats only showed light infections, 1 a moderately heavy one and in the remaining 9 very large numbers of the parasite were encountered.

Trichostrongylus vitrinus Looss, 1905 was by far the most common Trichostrongyle of the small intestine and was reported from almost half the number of goats harbouring worms. Here again the type of infection was classed as light, moderately heavy and very heavy, the

numbers of goats relating to each type being respectively 10, 7 and 11. This form, as well as *T. capricola* and *T. colubriformis*, when present in large numbers, gives rise to considerable enteritis and this condition was frequently met with in animals harbouring heavy infections of Trichostrongyles. Pure infections with a single species were comparatively rare and it was probable that the majority of cases of enteritis encountered were pathogenic conditions attributable to two or more *Trichostrongylus* species present in large numbers.

Trichostrongylus spp. were noted as light infections in 6 goats. In these animals the numbers of worms recovered were very small and did not include male specimens from which an accurate diagnosis of the forms present could be made. It is highly probable, however, that the female worms found belonged to one or other of the three *Trichostrongylus* species referred to above.

Capillaria longipes Ransom, 1911, the last of the small intestine forms which were found in the goats, was not very frequently met with and was recovered from 7 animals as light (5) and moderately heavy (2) infections.

(*c*) CAECUM AND LARGE INTESTINE :

Chabertia ovina (Fabricius, 1788) was the Strongyle form most frequently met with, occurring in 38 out of the 66 parasitized goats. Animals harbouring less than 25 worms per individual numbered 19, from 25 to 100 worms in 12 goats and over 100 worms were recorded from each of 7 hosts.

Oesophagostomum venulosum (Rudolphi, 1809), the other Strongyle from the lower region of the intestinal tract, was only slightly less common than *C. ovina* and was recovered from 32 goats. It did not, however, occur in such large numbers as the above form and produced only a single very heavy infection. The remaining cases comprised 19 light and 12 moderately heavy infections.

Trichuris ovis (Abildgaard, 1795) was the species most frequently encountered, not only amongst the parasites of the large intestine, but also amongst all the others recorded in this paper. Thirty-nine goats were found to harbour this whipworm, the numbers present in each animal extending over a wide range from a single specimen in 5 goats to as many as 178 individuals, counted in one of the heavily infected

animals. Briefly, the lightly infected goats numbered 27, while moderately heavy infections amounted to 7 and heavy infections to 5 cases.

Skrjabinema ovis (Skrjabin, 1915), a somewhat rare parasite of sheep and goats, was found on 3 occasions. It was first encountered in British goats by one of us (Morgan, 1930) and the species was re-described from material obtained from 2 kids which had been presented to the Institute from the South of England. Since the two goats had been kept on the observational plots at Winches Farm some months before being examined *post mortem* it was difficult to determine whether infection had occurred before or after their arrival. This Oxyurid was encountered by the other writer (J.N.O.), however, on a third occasion during the *post mortem* examination of a 6 months old kid. In this case it appears probable that infection occurred before the animal reached the Farm. It was given by a donor residing near Wolverhampton. Six days after birth and on arrival at the Farm it was placed in one of the indoor goat-pens and hand reared, at first, on a milk diet. Later its food consisted of bran, crushed oats and other farinaceous materials and it had access at no time to the outdoor paddocks where it might have been able to pick up an infection of *S. ovis*, if present. Practically no young stages of the parasite were found in the material collected, which consisted of well over 300 specimens, and this seemed to show that, at any rate, reinfection, which had occurred in the case of the two goats from which Morgan's specimens were obtained, was not present here. This third occurrence of *S. ovis* infection rather lends support to a previous observation (Morgan, 1930) that the parasite may be of long standing in this country but has not been found at all frequently owing to the comparatively little attention given to goat parasites.

Remarks.

It is interesting to record the fact that *Bunostomum trigonocephalum* (Rudolphi, 1808), a very common hookworm parasite in the small intestine of sheep in Britain, was not encountered at all in any of the goats examined. It is, however, known from goats in Scotland. Similarly, *Strongyloides papillosus* (Wedl, 1856) was not recorded from any of the goats. It is, nevertheless, a known parasite, not only of sheep, but also of goats in Britain and infections, which later died out, have been produced in goats kept at the Institute Farm.

It was seldom that goats were found to harbour pure infections of one species of worm and it was habitual for two or more up to nine different parasite species to be recovered from any one individual animal. The following shows this : 1 species was recorded from each of 6 goats, 2 species from 11 goats, 3 species from 10 goats, 4 species from 11 goats, 5 species from 10 goats, 6 species from 5 goats, 7 species from 4 goats, 8 species from 5 goats and 9 species from 4 goats.

As previously stated the dominant species was *Trichuris ovis* and this was closely followed by *Chabertia ovina* and *Ostertagia circumcincta*. These three species occurred in more than 50 per cent. of the goats found parasitized. Continuing in descending order of frequency the species found in more than 33 per cent. but less than 50 per cent. of the infected animals were *Oesophagostomum venulosum*, *Trichostrongylus vitrinus* and *Haemonchus contortus*. The remaining species were all recovered from less than 25 per cent. of the animals and were, following the descending scale of frequency, *Muellerius capillaris*, *Trichostrongylus capricola* and *T. colubriformis*, *T. axei*, *Nematodirus filicollis*, *Cysticercus tenuicollis* and *Capillaria longipes*, *Moniezia* spp., *Ostertagia trifurcata* and *Skrjabinema ovis*, while *Dictyocaulus filaria* and *Cooperia curticei* were each found on one occasion.

The incidence of these naturally acquired infections are probably higher in some cases than would be found amongst goats from other parts of the country since certain of the animals were used in experiments to test out the effects of heavy stocking on the worm burden under a system of rotational grazing. Some of the goats dying during the experiment, which was carried out by one of us (Morgan, 1933), were found to contain enormous masses of certain species of worms, particularly *C. ovina*, the Trichostrongyles of the small intestine and *O. circumcincta*, all of which appeared to be a contributory cause to the death of the goat, for death occurred in those animals with the highest worm burden.

It seems clear, however, that our knowledge of the distribution and frequency of occurrence of goat parasites, not only in Britain, but throughout the world should be extended and that reliable data concerning the intensity of infections should be made known especially with regard to the pathenogenic species. All the forms mentioned in this paper, with the exception of *Trichostrongylus capricola* and *Skrjabinema ovis*, are also common parasites of sheep and, in a less degree,

of cattle and deer, in Britain. It is thus evident that the goat may be considered as a potential focus of infection when kept on pastures frequented by these other domesticated animals, especially the younger ones in which the tissues seem less resistant and more intolerant of injury by worms.

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On *Syngamus nasicola* Linstow, 1899, from sheep and cattle in the West Indies.

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The validity of *Syngamus nasicola*, Linstow 1899, has been questioned on more than one occasion in the more recent publications on Syngamids in mammals, and there is a tendency to regard this species as synonymous with *S. laryngeus* Railliet, 1899. Von Linstow's somewhat inadequate original description—the only available one—agrees fairly well with Railliet's species both in the original account of the latter and subsequent re-descriptions of it by Sheather and Shilston (1920), Chapin (1925) and Ware (1925), and the fact that *S. nasicola* was described at about the same time as *S. laryngeus*, and apparently without knowledge of the latter's existence, has been adduced to support the theory that the two species are probably identical.

The hosts of *S. laryngeus* are cattle, buffalo and man, and the species has been recorded from widely distributed localities, viz. India, Malay, Philippines, Cochin China, Porto Rico and Brazil. *S. nasicola* was found in the goat in Cameroons and in deer in Brazil.

Whilst in the West Indies during 1932–33 the writer, at Professor Leiper's suggestion, examined the nasal cavities of ruminants in Trinidad, and found therein a species of *Syngamus* which differed in certain important characters from *S. laryngeus*, and for the correct identification of this form it was necessary therefore to reconsider the question of the validity of *S. nasicola*. Through the courtesy of Professor Arndt of the Berlin Natural History Museum, the writer was enabled to examine co-types of this species and to study it in relation to *S. laryngeus* and the species from Trinidad. The conclusions were subsequently arrived at that *S. nasicola* is a valid species, and identical with the Trinidad material.

In his original account of *Syngamus kingi* from a human case in St. Lucia, British West Indies, Leiper remarked the resemblance between

it and *S. dispar* from *Felis concolor* and suggested that some domesticated animal such as the cat or dog might be the normal host of this apparently abnormal human parasite. The writer is publishing later a description of a new species of *Syngamus* which was found frequently in the nasal cavities of domestic cats in Trinidad, and points out its dissimilarities to *S. kingi*. The resemblance however between *S. nasicola* and *S. kingi*, the holotypes of which were kindly lent by Professor Leiper for comparison, are highly suggestive that these two species are identical. If this be so, then *S. kingi* becomes a synonym of *S. nasicola* which consequently must be regarded as a potential human parasite.

The following descriptions from which the above conclusions were deduced, are based upon four lots of material. (1) *S. nasicola* from West Indian sheep and cattle, (2) *S. nasicola* co-types from deer (Brazil) and goat (Cameroons), (3) *S. kingi* holotypes from man (St. Lucia) and (4) *S. laryngeus* from cattle (Malay).

S. nasicola from West Indian Sheep and Cattle.

Of eighteen sheep examined, ten (i.e. 55·5 per cent.) were found harbouring the worms in the nasal cavities or were passing the typical *Syngamus* eggs. In one sheep, said to have come from St. Vincent, an unusually large number of worms was present, seventy-six pairs in all, and were situated in the pharynx and trachea as well as in the nares. Specimens were taken from the pharynx of two out of twenty cattle examined, and a third was positive by faecal examination alone, giving a 15 per cent. infection in cattle. One of three goats, by faecal examination was found to be infected with *Syngamus*, and it is presumed that this is the same species as that of the sheep and cattle.

Female.

The body tapers gradually to either extremity from the vulvar region at which it has its greatest diameter. The length varies from 11·4 to 23·5 mm., and the average of 28 specimens was 17·1 mm. The distance of the vulva from the anterior end of the body varies from $\frac{1}{3}$ to $\frac{1}{4\cdot3}$ of the total length of the body, the average of 27 measurements giving the fraction $\frac{1}{3\cdot8}$. The length of the oesophagus (including the buccal capsule) varies from $\frac{1}{8\cdot3}$ to $\frac{1}{15\cdot7}$ of the body length, the average of 26 measurements being $\frac{1}{12}$. The cervical papillae are protuberant, and their position is rather variable. They may be said to be situated at any point between the middle and posterior levels of the oesophagus.

Only in specimens in which the body cuticle was obviously shrunken were they found anterior to the middle, and were never found posterior to the posterior level. The excretory pore is usually very slightly anterior to the level of the cervical papillae. A pair of cervical glands stretch

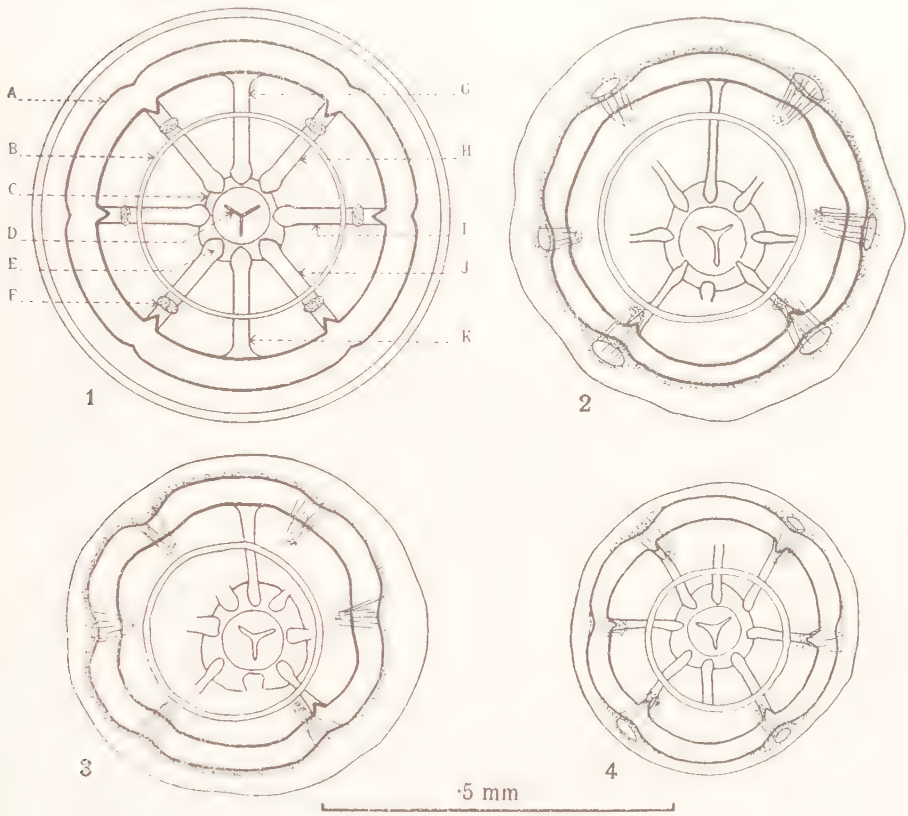
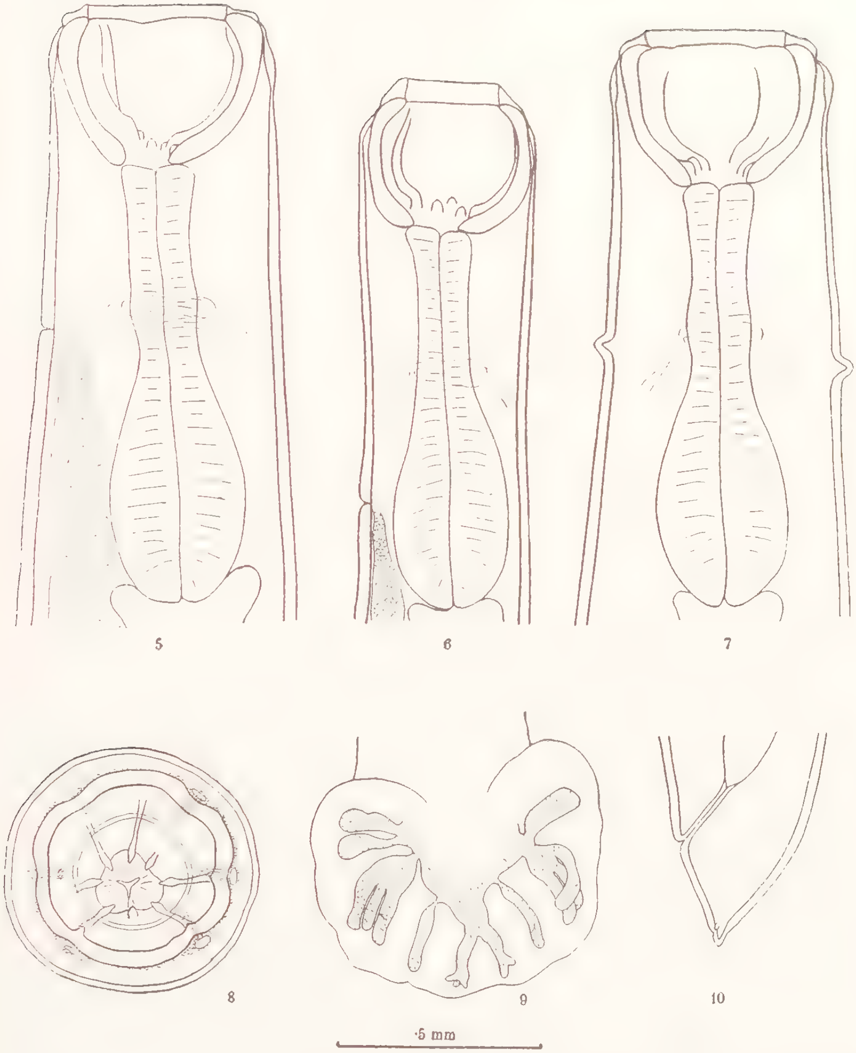


Fig. 1.—Diagram of end-on aspect of a Syngamid buccal capsule.

a. Buccal capsule wall.
b. Margin of oral aperture.
c. Oesophagus.
d. Lumen of oesophagus.
e. Sub-ventral tooth.
f. Sub-ventral oral papilla.
g. Dorsal rib.
h. Sub-dorsal rib.
i. Lateral rib.
j. Sub-ventral rib.
k. Ventral rib.

Fig. 2.—Buccal capsule of *S. nasicola* from *Bos taurus*, Trinidad.
,, 3.—Buccal capsule of *S. nasicola*, cotype from *Cervus rufus*, Brazil.
,, 4.—Buccal capsule of *S. laryngeus* from *Bos taurus*, Malay.

some distance posterior to the oesophageal region. The tail is short, 0·19 to 0·42 mm. long and bears a pair of minute papillae very close to the extreme tip. In lateral view the buccal capsule is seen to be considerably broader than long, i.e. shallow, the maximum dimensions exhibited by this organ being 0·4 mm. long by 0·58 mm. broad. Its opening to the oesophagus is offset slightly to the ventral side of the body. The buccal teeth, ribs and oral papillae are best seen from the end-on aspect, which is easily obtained by cutting off the end of the worm just behind the anterior end of the oesophagus and mounting the portion in the required position. From this aspect (Fig. 2) the capsule wall is seen to be indented regularly, though not equidistally, at six points, which divide its optical margin into six sectors which have a definite relation to the longitudinal axis of the body. Thus, two of the sectors, the longest of the six, are respectively dorsal and ventral in position. The remaining four all about equal to each other in length, are sub-lateral. It follows therefore that two of the indentations are strictly lateral, while the remaining four are arranged two sub-ventrally and two sub-dorsally. The six oral papillae, which are difficult to discern, are situated close to the margin of the oral aperture and correspond in position with the six indentations of the capsule wall. At the base of the buccal capsule there are eight teeth, arranged in a circle, more or less equidistally from one another, as follows: one dorsal, two sub-dorsal, two lateral, two sub-ventral and one ventral. From each tooth a rib extends up the capsule wall to a greater or less degree. It was found that the length of the ribs is of great importance in diagnosis, and hence special attention is given to this point in the description of the species. The number of ribs which extend from the teeth to the anterior margin is generally three. Occasionally the number is two or four, but has never been found to exceed four. The situation of the typical three ribs is one dorsal and two sub-ventral. The remaining five ribs are generally unequal and variable in length up to about half the distance up the capsule wall, or one or more of the ribs may be absent. In the case of the two sub-ventral ribs, they are seen at the anterior margin (in end-on view) as a V-shaped prominence on the inner surface of the capsule wall. In the case of the dorsal rib there is no prominence; at this level the rib flattens out flush with the surface of the capsule-wall.



S. nasicola from Sheep, Trinidad.

Fig. 5.—Anterior end of female, lateral aspect.
,, 6.—Anterior end of male, lateral aspect.
,, 7.—Dorso-ventral view of female.
,, 8.—Buccal capsule, end-on aspect.
,, 9.—Bursa of male, flattened out.
,, 10.—Tail of female, lateral aspect.

With regard to the genital organs, the vagina is very short and soon branches into two uteri, which run forward for a short distance and then bend posteriorly. The uterine coils themselves however extend a considerable distance on either side of the vulvar region but generally more so posteriorly than anteriorly. Posteriorly they are not usually found extending beyond the middle of the body. The ovarian tubules may extend forward as far as the oesophagus or back to within a short distance of the anus, but in no case were they found to reach the anus. (Fig. 11). The eggs are about $98 \times 54\ \mu$ and the surface of the shell is very faintly striated transversely. When passed in the faeces they are usually in the two-cell stage of development. Unlike the eggs of *S. trachea*, there are no polar caps.

Male.

The body tapers very slightly from the bursa to the head and measures 4 to 6·3 mm. in length. The average of 28 specimens was 4·9 mm. The buccal capsule is up to 0·31 long by 0·39 mm. broad and is relatively deeper than in the female. The teeth, buccal ribs and other parts of the capsule are similar to those described in the female, as are also the cervical papillae, excretory pore and cervical glands. Expressed as a fraction of the body length the oesophagus varies from $\frac{1}{3\cdot2}$ to $\frac{1}{4\cdot9}$, the average of 27 measurements being $\frac{1}{4\cdot2}$. The testicular tube loops one or more times and extends beyond the middle level of the body. The bursal rays have the typical arrangement and are short and stumpy. The ventrals as a rule are paired, but may be fused to form a single thick ray. The lateral rays lie close to one another and arise from a broad common part which is connected by a narrow stem to the body proper. The medio-lateral ray is shorter than its fellows. The externo-dorsal rays have each a narrow stem and arise separately from the dorsal ray. The dorsal ray is cleft for more than half its length and each branch is bi- or tri-digitate. A very careful search was made for spicules, after clearing the worm (detached from the female) in creosote, and also by dissection, but none were found.

S. nasicola Linstow, 1899. Co-types from Deer and Goat.

This material consisted of four pairs from *Cervus rufus* (Brazil) and two pairs from *Capra hircus* (Cameroons). The specimens from *Capra hircus* were much shrunken and distorted, and remained opaque even

after some time in a clearing agent, so that general measurements of these specimens would be valueless. The buccal capsules however were rendered transparent in beechwood creosote and appeared to be normal. In one pair they measured 0·375 long by 0·495 mm. broad in the female, and 0·3 by 0·315 mm. in the male. In the second pair they were 0·39 by 0·52 mm. in the female and 0·31 by 0·36 mm. in the male. In lateral view the buccal ribs seemed to have the same arrangement as in the West Indian material just described, and this was confirmed by an end-on view of the capsule of one of the males, obtained after some difficulty by standing the worm up vertically in the clearing liquid.

Of the four pairs from *Cervus rufus*, two were in excellent preservation and showed the following dimensions :—

First pair.—*Female.*

Length 21·07 mm. by 0·705 mm. in maximum diameter. Oesophagus 1·4 mm. = $\frac{1}{15}$ of body length. Vulva 4·65 mm. from the anterior end, = $\frac{1}{4\cdot5}$ of body length. Tail (with sub-terminal papillae) 0·375 mm. long, = $\frac{1}{56}$ of body length. Cervical papillae and excretory pore, a little behind the middle level of the oesophagus. The buccal capsule measured 0·405 long by 0·57 mm. broad and in its lateral view it is seen that the typical arrangement of the buccal ribs is present, i.e. two sub-ventral and one dorsal. The distribution of the genitalia is seen in the diagram.

Male.

Length, 5·25 by 0·405 mm. broad. Oesophagus 1·23 mm. = $\frac{1}{4\cdot3}$ of body length. Buccal capsule 0·33 by 0·42 mm. broad. The bursal rays could not be studied as it was undesirable to risk injuring the specimen in attempting to detach it. Cleared in creosote, no spicules could be seen.

Second pair.—*Female.*

Length 13·8 mm. Oesophagus 1·05 mm. = $\frac{1}{13\cdot1}$. Vulva 3·45 mm. from anterior end, = $\frac{1}{4}$. Tail (with papillae) 0·28 mm. Buccal capsule 0·32 by 0·452 mm. broad. Ribs as in 1st specimen. Two uterine eggs, taken at random, measured respectively, 92 × 48, and 96 × 50 μ.

Male.

Length 3·15 mm. Oesophagus 0·9 mm. = $\frac{1}{3\cdot5}$. Buccal capsule 0·28 long by 0·328 broad. No spicules were found.

In a third pair the female was found considerably damaged and the head of the male was cut off and mounted in balsam, so that an end-on view could be obtained. In this specimen it is seen (Fig. 3) that only two of the ribs are complete, viz. one sub-ventral and the dorsal rib. The other sub-ventral only reaches halfway up the capsule ; there is one short lateral, and the remaining four teeth appear to have no ribs.

Although from different hosts and differing widely in their geographical distribution it seems that the two lots of material comprising Linstow's types, are one and the same species, for in the important characters of the structure of the buccal capsule they certainly agree. Linstow's description of *S. nasicola* is briefly as follows :—

Female 20·6 mm. long by 0·87 mm. broad. Oesophagus $\frac{1}{51}$ (!) of body length, and tail $\frac{1}{52}$. Vulva divides body in the ratio of 3 : 10. Eggs 88 × 46 μ.

Male 5·6 mm. long by 0·47 mm. broad. Oesophagus $\frac{1}{4\cdot6}$ of body length. Buccal capsule 0·32 mm. long by 0·48 mm. broad, supported by six longitudinal ribs.

Syngamus kingi, Leiper, 1913.

This species is represented by a female and a male which have been detached from one another. The buccal ribs, as illustrated in Leiper's original figures, conform with the arrangement described in *S. nasicola*. The *female* is 14·9 mm. long, and the vulva is 3·75 mm. from the anterior end, $= \frac{1}{3\cdot97}$ of body length. Oesophagus 1·2 mm., $= \frac{1}{12\cdot4}$. The tail is bluntly conical, 0·25 mm. long, and a very short piece is broken off the tip so that terminal papillae are not visible. The buccal capsule is 0·54 mm. in lateral diameter, and 0·39 mm. long, giving a ratio of 1 : 1·38. The vagina is short and branches soon into two uteri which run forward for a short distance and then curve posteriorly. The uterine coils extend nearly to the middle of the body, and the ovarian tubules to about the junction of the posterior and second fourths of the body (see diagram). An agglomeration of intestinal cells near the anus resemble immature ova. The *male* is 3·5 mm. long by 0·25 mm. broad. Oesophagus 1·1 mm. $= \frac{1}{3\cdot2}$ of body length. Buccal capsule 0·42 mm. in lateral diameter by 0·32 mm. long, giving the ratio 1 : 1·3. The bursa is of the usual stumpy type with a bifurcated dorsal ray, each ray being digitate at its tip. Medio-lateral ray shorter than the adjoining laterals. Ventrals stumpy and fused into one on the right side. Externo-dorsals arising rather far from the dorsal ray. Spicules are apparently absent.

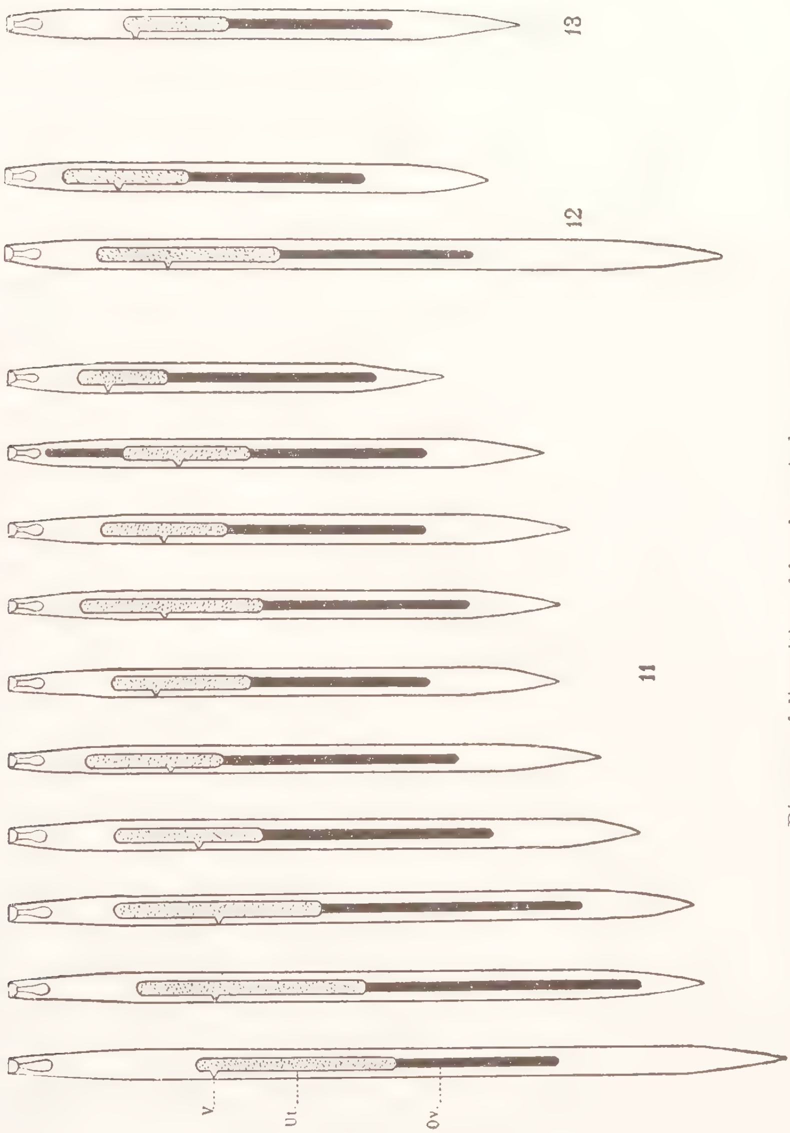


Diagram of disposition of female genital organs.

Fig. 11.—*S. nasicola* from sheep. Fig. 12.—*S. nasicola* cotype from Deer. Fig. 13.—*S. kingi* holotype from Man.

Syngamus laryngeus, Railliet, 1899.

This material consists of two pairs in copula, from Malay cattle, from a collection sent by Dr. Daniels in 1900, and now in the Helminthology Department of the London School of Hygiene and Tropical Medicine. Since they are both about the same size and appearance, a description of one will suffice. The state of development of the eggs in the uterus suggests that the specimens are not quite mature.

Female.

Length 9·7 mm. by 0·45 mm. broad. Vulva 2·4 mm. from anterior end, $= \frac{1}{4}$. Tail 0·18 mm. with indistinct papillae near the tip. Oesophagus 1·27 mm. or $\frac{1}{7 \cdot 58}$ of body length. Cervical papillae and excretory pore in advance of the middle of the oesophagus, but this is unreliable as the body cuticle in this region is somewhat shrunken. In other descriptions it is said to be near the middle level of the oesophagus. Buccal capsule 0·47 mm. broad by 0·4 mm. long, giving the ratio 1 : 1·175. In lateral or dorso-ventral view six ribs are easily seen extending from the teeth up to the margin of the capsule, and two extending about half-way up. In end-on view (Fig. 4) this arrangement is seen still more clearly. The six indentations of the capsule and the corresponding six segments are similar to those described in *S. nasicola,* the dorsal and ventral segments being the longest of the six. Extending towards these two segments, half-way up the wall are the dorsal and ventral ribs, the remaining six extending up to the anterior margin and appear as six V-shaped prominences on the inner surface of the capsule wall. This arrangement, which has been observed by Sheather and Shilston and Ware in their Indian representatives of *S. laryngeus,* constitutes the most striking and definite difference between this species and *S. nasicola.*

Male.

3 mm. long by 0·4 mm. broad. Oesophagus 1·1 mm. $= \frac{1}{2 \cdot 7}$. Buccal capsule 0·38 broad by 0·32 mm. long with a similar buccal capsule structure to that of the female. The spicules are unequal, being 24 and 28 μ long and although difficult to see, were found after clearing the specimen in creosote, but without dissecting or detaching it from the female. The bursal rays are hardly visible in this material, with the exception of the laterals on one side which are about equal in length and close to one another.

Discussion.

The genus *Syngamus*, as represented by the known mammalian species presents considerable difficulties in differential diagnosis. The dimensions of the worms themselves and their organs are subject to such variations that overlapping necessarily occurs in different species, and makes identification by such means risky and unreliable. In structure also, in some of the organs at any rate, there is a lack of specificity or a range of variability which renders these useless in the differentiation of species.

In the case of the earlier discovered species, descriptions of them are based much on general lines, and were it not known to what hosts these species belong, in the absence of the type material subsequent identifications would be almost impossible. Until recent years, the paucity of the known species of mammalian Syngamids and the consequent incompleteness of our knowledge of this group, has been another obstacle in the way of differential diagnosis. As with other nematode groups, however, with the advent of additional species and adequate material for study, the correct estimation of the value of structure and dimension becomes possible and results in the formation of new criteria of diagnosis.

In the case of *S. nasicola* and *S. laryngeus* it is evident that such characters as length of body, length or relative length of oesophagus, position of vulva, length of ♀ tail, and relative position of ♀ and ♂ buccal capsules are of little use individually in demarcating the two species. The relative length of the oesophagus in the female, $\frac{1}{7 \cdot 58}$ as against $\frac{1}{8 \cdot 8}$ to $\frac{1}{15 \cdot 7}$ in *S. nasicola* suggests that this character might be of specific value, but Ware gives a range of $\frac{1}{8}$ to $\frac{1}{18}$ in his *S. laryngeus* material. Insufficient data is to hand in the case of *S. laryngeus* as to the bursa and the maximum dimensions of the buccal capsule in the female for these characters to be evaluated correctly, but possibly they will subsequently be found to be of specific value. There remain then three characters on which the differential diagnosis of the two species can be based, viz. (1) the internal structure of the buccal capsule, (2) the ratio of length to breadth of the buccal capsule and (3) the presence or absence of spicules.

With regard to spicules there is some doubt. The writer has no hesitation in stating that in *S. nasicola* from the West Indies spicules are absent, and in this character it differs from *S. laryngeus* in which

they have been shown to be present in material from different sources by different workers. They have been noted by Ware in material from buffaloes and cattle in Muktesar, India; by Chapin in specimens from *Bos taurus* from other localities; and by the writer in specimens from Malay cattle. De Does (1907) mentions that two are present in material identified tentatively as *S. laryngeus.* (The end-on view of a buccal capsule figured by De Does is not, in the writer's opinion, that of *S. laryngeus.*) Railliet was unable to find spicules and Sheather and Shilston state that they are absent. Owing to their very small size, however, an erroneous negative finding would be excusable and it seems justifiable to assume that spicules are always present and characteristic of *S. laryngeus*, which in this respect therefore differs specifically from *S. nasicola.*

As to the relative dimensions of the buccal capsule in the two species under discussion, it appears from available descriptions that this structure is broader than long, i.e. shallower in *S. nasicola* than in *S. laryngeus.* The ratio of length to breadth of the female capsule in *S. laryngeus* from Malay (Daniel's material) is 1 : 1·175 in one specimen and 1 : 1·083 in the other. Ware figures a female capsule as about 0·46 mm. long by 0·41 mm. broad, which gives the ratio 1 : 0·89. These are the only data the writer has been able to collect regarding the dimensions of the female capsule of *S. laryngeus.* Compared with *S. nasicola* there is a striking difference. Of nine females from Trinidad sheep and cattle the minimum ratio was 1 : 1·27 and the maximum 1 : 1·55. The average ratio of the nine was 1 : 1·36. In Linstow's material the ratios were for the specimens from *Cervus rufus*, respectively 1 : 1·4 and 1 : 1·52; and from *Capra hircus*, 1 : 1·32 and 1 : 1·33.

In commenting upon Linstow's description of *S. nasicola*, Chapin remarks that there is only one point in it which serves to distinguish it from *S. laryngeus*, viz.: the proportional dimensions of the male capsule which are given as 0·32 mm. deep by 0·48 mm. in breadth. Chapin argues that if the capsule measured was really that of the male, then the female capsule should be very shallow and that therefore the two species are probably distinct. Unless Linstow measured the depth of the capsule *internally*, Chapin's implied suggestion that the figures really appertain to the female capsule, is probably correct, for the writer's measurements of the cotypes give the greatest ratio of length to breadth

as 1 : 1·27 in the male capsule, which differs greatly from Linstow's figures which work out at 1 : 1·5. Although Chapin does not give detailed measurements of the female capsule of *S. laryngeus* he states that its dimensions approximate to those of the male of *S. nasicola* as given by Linstow. This would appear to dispose of the writer's hypothesis that the ♀ capsule of *S. nasicola* is shallower than that of *S. laryngeus*, but more comprehensive data are required in order to clear up this point definitely.

The third character on which the differential diagnosis of *S. nasicola* and *S. laryngeus* is based, viz. : the internal structure of the buccal capsule, is the most important, since it seems to be well-defined and constant, and leaves little doubt as to the separate identity of the two species. Railliet's statement that eight of the ribs reach the margin of the capsule seems doubtful, since subsequent examinations of similar material have shown the dorsal and ventral ribs are constantly shorter than the others, as indicated by Ware, Sheather and Shilston and the writer. Linstow's account of six longitudinal ribs in *S. nasicola* is unfortunate since it immediately implies identity with *S. laryngeus*. Since, however, nothing is said as to the length or extent of the ribs, and in view of the writer's re-examination of similar material, this does not constitute a serious objection to the specificity of the ribs in the two species.

With regard to the identity of *S. kingi* there can be little doubt but that this species and *S. nasicola* are one and the same. In the important characters of the buccal capsule they agree, both in the relative dimensions of the organ and in the internal structure, although an end-on view of this was not feasible. Spicules are apparently absent from *S. kingi* and its general dimensions fall with the range of those of *S. nasicola*. Chapin has pointed out that *S. laryngeus* differs from *S. kingi* in that the genitalia in the latter reach nearly to the anus. This would similarly be a point of difference between it and *S. nasicola* if the character were as so defined, but in the above description it has been pointed out that the genitalia do not extend so far posteriorly. In view of its strong resemblance to *S. nasicola* the question of the possible identity of *S. kingi* with *S. dispar*, whose morphology is not well known, hardly arises, and further it has been shown to be distinct from two other feline species, *S. felis*, Cameron, from the Malay tiger, and a new species from domestic cats in Trinidad.

As to the question of the normal host in St. Lucia, the writer failed to find *S. nasicola* in ten sheep examined in St. Lucia, but it seems probable that it is or has been there, since it is present in the neighbouring island of St. Vincent, only thirty miles distant.

Five other cases of Syngamosis in man are on record. Travassos (1922) reported a case in Brazil, in which the worms were identified as *S. laryngeus*. St. John, Simmons and Gardner (1929) reported a human case in the Philippines, which has also been ascribed to *S. laryngeus*. (See in Hoffman, 1931.) Hoffman (1931 and 1932) gives accounts of two cases in Porto Rico in which the parasites involved were identified as *S. laryngeus*, and in an addendum to his later publication gives information regarding an unidentified case of human Syngamosis in Trinidad. It is apparent therefore that both *S. laryngeus* and *S. nasicola* are potential human parasites, and that sheep and cattle are new hosts for the latter species.

With regard to the geographical distribution of these two species, the possibility suggests itself that owing to the previous lack of information regarding *S. nasicola*, the species may have been confused with one another and hence our knowledge of their distribution may be faulty. More complete and accurate data on this subject might lead to interesting conclusions, for the available, if somewhat meagre information, suggests that *S. nasicola* is a New World and African species and that *S. laryngeus* belongs to the Indo-Asiatic area.

Summary.

1. The occurrence of *Syngamus nasicola* Linstow, 1899, in sheep, cattle and goats in the West Indies is recorded.
2. The species is re-described, on the basis of West Indian material and cotypes from deer and goat.
3. The species is contrasted with *S. laryngeus* Railliet, 1899, with which it has affinities and has hitherto been thought to be identical.
4. Special emphasis is laid on the use of the internal structure of the buccal capsule in differentiating the two species.
5. *Syngamus kingi* is compared with *S. nasicola* and it is concluded that the two species are identical, in which case *S. kingi* becomes a synonym of *S. nasicola*.

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